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GENETICS AND THE PHYSIOLOGY OF DEVELOPMENT¹

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THE Sedgwick Lecture, given this year at Woods Hole, where physiologists, embryologists and even geneticists are foregathered, seems a suitable occasion to discuss some of the problems common to the three fields of research. For another reason, too, the occasion seems propitious. Professor Sedgwick, to whose memory these lectures are dedicated, always took a very broad interest in physiology. This interest extended beyond the field of traditional human physiology into the widest biological aspect of physiology, both theoretical and practical.

The modern theory of genetics may seem, at first sight, to concern itself with methods quite foreign to those of physiology. Genetics deals with ratios between classes of related individuals that appear in successive generations in crosses between two types differing in one or more characters. There is nothing in this procedure that seems to appeal to physiological processes in the individuals in question—in fact, it seems rather to ignore them.

That the process of segregation and crossing-over, as interpreted in terms of chromosome maneuvers, is, in the ultimate analysis, the outcome of physiological processes

¹ The William Thompson Sedgwick Memorial Lecture. Given at Woods Hole, Mass., on July 27, 1926.

in the cells, goes without saying. Nevertheless, geneticists seem, as I have said, to get along very well, with little or no physiology, in the conventional sense of that term; but in the literature it will be found that they have not infrequently committed themselves, sometimes unwittingly, to views that have fundamental physiological implications.

It is quite true that a purely numerical treatment of the phenomena of genetics can be given that is adequate to meet the genetic situation. It is also true, I think, that there is some risk in departing from the exactness that the genetic method insures by embarking on speculations as to the physiological processes lying behind the phenomena of genetics.

On the other hand, while there are undoubted advantages in a purely numerical treatment of genetics, it is, nevertheless, true that these advantages may be offset by the desirability sooner or later to trace back the long chain of connections between the somatic characters and the postulated units in the germ-cells.

GENES AND CYTOPLASM

There has been some criticism of the theory that the genes are the exclusive factor in heredity, on the grounds that the cytoplasm can not be ignored in any complete theory of heredity. There is no need, I think, for misapprehension on this score. The confusion that is met with sometimes in the literature has resulted from a failure to keep apart the phenomenon of heredity, that deals with the transmission of the hereditary units, and the phenomena of embryonic development that take place almost exclusively by changes in the cytoplasm.

It is not necessary to elaborate these questions here, since they have been stated and restated many times; but in order to avoid misunderstanding I may be permitted to make one brief comment. There are bodies in the cytoplasm (such as the plastids of which the chlorophyl

bodies are most familiar examples) that increase automatically and fulfil in this respect the general requirements of heritable materials in a general sense. They are transmitted through the cytoplasm of the egg, and in special cases, in plants at least, possibly through the pollen grains. In both cases they are inherited but not with the precision of the genes. There has never been any serious attempt to ignore this kind of heredity, though it has seemed to me desirable to keep it in a chapter by itself.

It may not appear far-fetched to assume that there may be other bodies in the cytoplasm that grow and divide and, by extension, it might not seem too extravagant to assume that the protoplasm itself (except for its secretion products) consists of units that grow and divide and are inherited. No one will, I think, deny this as a possibility, but it is surprising to find that those who advocate this view (or cast a longing eye in this direction) overlook one of the best established results of genetic work. It is thus that, except for the rare cases of plastid inheritance, the *inheritance* of all known characters can be sufficiently accounted for by the presence of genes in the chromosomes. In a word the cytoplasm may be ignored genetically.

On the view that the cytoplasm consists of self-perpetuating units, the genetic conclusion just stated may mean that cytoplasmic bodies are under control of the materials set free by the genes and that at present we have no means of studying this passive inheritance through the cytoplasm. On this view the same cytoplasmic genes would be everywhere present in all the cytoplasm of each species. In fact, it has been suggested that it is a peculiarity of different species that they are made up of specifically different proteins, possibly confined to the cytoplasm. Fortunately, there is a test for these assumptions that seems to be crucial. It is not new and has been known nearly one hundred years to botanists, if not to all physiologists. Species when crossed

reciprocally give generally identical hybrids. When the cross is made one way the cytoplasm comes from one species, when the cross is made the other way the cytoplasm comes from the other species. If the cytoplasm is specific, the hybrids should be different, but since they are identical, the cytoplasmic hypothesis is disproven or at least can be ignored until further evidence is forthcoming that the constitution of species rests on specifically different proteins that reside *only* in the cytoplasm.

SOME APPLICATIONS OF GENETICS TO PHYSIOLOGICAL PROCESSES

One of the most valuable contributions that genetics has made to the physiology of development is the recognition of the need of using homogeneous—*i.e.*, homozygous, materials.

It has long been known that the environment is one of the causes of variability in embryological development, even within the range of changes that are normal. It had not been so well appreciated, until genetics made the situation clear, that genetic elements may produce effects that superficially at least are often indistinguishable from those produced by the environment. Here, then, are two variables producing like results. Now, the most promising lead that we have at the present time in the study of development of the living organism is to vary the environmental conditions—especially the temperature—in order to get data as to the nature of the processes that are taking place. Unless the other variable—the genetic constitution—is under control it is hopeless to try to get reliable data.

It is sometimes taken for granted that wild types give uniform material, but we know this is not always the case, for, while there may be a better chance that wild types are genetically more homogeneous than are domesticated animals and plants, it is very unsafe to take too much for granted in this connection. One hears it said sometimes, by those working with statistical methods, that by using

litter-mates a sufficiently controlled material is obtainable. We know that this is not the case. Litter-mates may be as different, from a genetic point of view, as any two other individuals of the race. It is true that there may be a slightly better chance, if litter-mates are used, of obtaining nearly similar individuals, but unless animals have been long inbred, this sort of material is not sufficiently good for exact physiological work, whether that work is on embryos or on adults.

By way of illustration let me briefly run over a few instances where the need that the material be fully controlled from a genetic point of view is obvious.

Johannsen's selection experiment with the Princess Bean is a classic case in point. The success of that experiment depended on the fact that this plant propagates by self-fertilization and in consequence each plant had automatically become homozygous in all its genes. Hence, although reduction of the chromosomes takes place, all the sperm and all the eggs have identically the same genetic make-up. With this genetically pure material, Johannsen was able to carry out a clean-cut experiment in selection—something that had never been done before—and in consequence he was able to demonstrate the stability of the gene. The whole outlook of variation in relation to natural selection was for the first time put on a scientific basis. By eliminating one of the variables, the genetic one, Johannsen obtained accurate data for a study of the other variable, *i.e.*, the environment.

Another illustration as to the necessity of using homozygous material is found in East's recent work on self-sterility in tobacco. It was long suspected that self-sterility in plants depended on genetic factors, but it was difficult or impossible to prove this, when more than a single factor difference was present, until homozygous material was obtained. This seemed impossible because self-sterility itself prevented it.

East found that certain self-sterile plants could be self-fertilized if pollen was placed on the stigma before the

flower opened. Using such a technique for ten or more successive seasons, he finally obtained lines that were approximately pure. With this material he then proved by breeding tests that genetic factors for self-sterility were present. He proved, moreover, that the results were determined by the rate of growth of the pollen tube, which, in turn, is probably determined by an enzyme action between materials in the pollen tube and in the tissues of the style.

That differences in the degree of immunity to certain diseases, both in plants and animals, are due to genetic as well as to environmental influences is known. It will be necessary, for exact work in these fields, to employ homozygous material. This applies, no doubt, in equal degree in the study of cancer, both as to its incidence as well as in experimental transplantation in a study of the reaction of the host. All this is gradually becoming apparent to those working in these fields.

These illustrations relate to the practical application of genetic principles to problems that are essentially physiological but where the actual physiological processes involved are not well understood. A nearer approach is found in problems relating to vigor as shown, in rate of growth and in size. What is known as hybrid vigor is perhaps the most interesting side of this question in the present connection. It has long been known to breeders of corn that outcrossing is essential for high production, which means, amongst other things, rapid and continued growth.

Several explanations have been proposed to explain hybrid vigor. We need no longer consider seriously an ancient and mystical conception that the act of union of two germ-cells rejuvenates the product of union (whatever that delightful phrase may mean), for one side of the problem at least has now been definitely brought into the field of genetic research.

One of the earliest interpretations of hybrid vigor was that it is due to the heterozygous condition of some or many of the genes. This interpretation is consistent with

the variability in vigor shown by the following generations, which, through inbreeding, become progressively less heterozygous and less vigorous. There are, however, certain theoretical objections to this interpretation, and another more plausible explanation of the facts may now be given. It has been pointed out, for instance, that, as a result of long cultivation, many recessive mutant genes have accumulated in cultivated races of corn and that some, or many of these, affect the vigor adversely. When two races, carrying different recessive genes, are crossed, the gametes of each race bring in some of the wild type genes (which are assumed in large part to be dominant). Hence the hybrid returns to the full vigor of the race, because it has recovered half of its original inheritance, and since this half contains the dominant genes, the effect approaches the original vigorous condition.

If now such a recovered type (F_1) is self-fertilized many recombinations of genes occur. A wide range of individual vigor is expected and found. Further inbreeding will tend to establish strains made up again, in part, of double recessive characters and this explains the fall in vigor.

This interpretation, however, still leaves certain important facts unexplained. For instance, if the increase in vigor is due to the presence of dominant factors then the double dominants obtainable in the second generation might be expected to be at least as vigorous as the heterozygotes. Individuals should then be obtainable whose vigor is not reduced by inbreeding.

Moreover, there would be in the second generation an asymmetrical distribution of vigor whenever heterosis is exhibited in the first generation.

These expectations are based, however, on the assumption that all the dominant genes in question freely segregate, but at the present time we have come to realize that, owing to linkage, this is not to be expected. Taking linkage into account the kind of results that are obtained can probably be explained.

Here, then, we have what appears to be, and is fundamentally, a physiological problem, but one that needs first to be put into shape by the methods of genetics before it is simple enough for direct physiological study.

ENVIRONMENT AND GENETICS

Before proceeding further, it may be in order to say a word concerning the relation of environmental factors to genetic factors.

It hardly seems necessary to explain to a group of physiologists that the environment is one of the essential factors determining the kind of physiological reaction that takes place, but a few illustrations will serve at least to show that geneticists are perfectly aware of this relation.

There is a mutant race of *Drosophila* in which the pigment bands on the abdomen are extremely irregular or are absent altogether. As long as the food conditions are favorable flies of this kind emerge, but when the external conditions become less and less favorable, the pigment bands tend to become more and more normal, until at last all the flies that emerge are indistinguishable from normal ones. If abnormal abdomen is crossed to normal and an F_2 reared, a good three to one ratio is obtained—three abnormals to one normal—provided the conditions are favorable—that is, if there is plenty of food, the cultures are moist and no crowding occurs. If, however, external conditions are poor, there may be no flies with abnormal segments in the second generation.

Another illustration may bring the matter nearer home to zoologists because it is one in which symmetries and reduplications of highly elaborate structures are involved—"forms" that transcendental morphologists regard as *fundamental* in the sense of being rather sacred. There is, for instance, another race of *Drosophila* that often has one, two, or even all its legs doubled—even down to the base. This race differs from the normal by a single gene, but the character appears only when the flies are reared

in an ice chest. If the experiment is carried out sufficiently near the freezing point, good Mendelian ratios are obtained; if at room temperature no flies result with more than six good legs.

With facts like these before him the geneticist should be the last person in the world to overlook the influence of the environment on the development of characters.

The sex-chromosome mechanism furnishes perhaps the most illuminating illustration of the relation of genetic and environmental influences. In most of the higher animals in which two sexes occur, and in some, at least, of the flowering plants, a mechanism exists that automatically produces two kinds of individuals. These are, as a rule, sharply marked off without intergrades, and little subject to environmental effects in so far as the essential production of eggs, or of sperm-cells, is concerned. The mechanism works, as you know, on the plan that one sex is di-gametic. Of the two kinds of gametes produced by this sex, one has an X-chromosome and the other a Y-chromosome. Since the opposite sex produces only one kind of gamete, each gamete carrying an X-chromosome, there result, on random fertilization, two kinds of individuals, XX and XY, in every generation (Fig. 1).

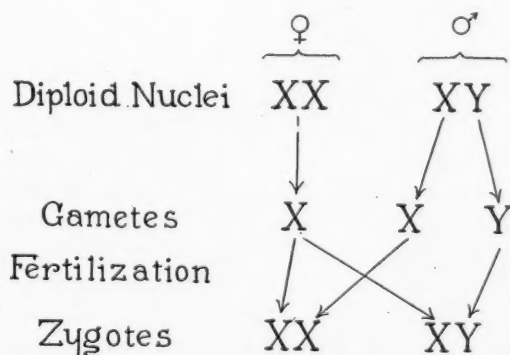


FIG. 1.

As I have said, this mechanism works automatically under a wide range of environmental conditions. In most cases, therefore, the possible influence of the environment may be ignored. Nevertheless, there is no more reason in this case than in any other to suppose that the environment may not under certain conditions reverse the end-result.

In fact, in a few cases, and under special conditions, it has been found that an individual that has the genetic make-up of a female may develop both eggs and sperm. These rare cases have, at times, been heralded as destructive of the chromosome theory of sex-determination. But this is a superficial criticism showing a complete misunderstanding of the genetic interpretation of the chromosome mechanism.

It may be frankly admitted that geneticists, who have advocated the chromosomal mechanism of sex determination, have not always taken the pains to guard their advocacy by the reservations of stated environmental conditions, but this scarcely gives sufficient grounds for the criticism, that, when sex reversal occurs under exceptional conditions, the theory of a chromosomal mechanism has been overturned. Such violent and extravagant statements are, in the long run, likely to react on those who indulge in them.

Fortunately, there is a genetic method by which these physiological reversals of sex can be put to a crucial test, and the two best cases of reversal that are known have, in fact, been subjected to the test, and both have given favorable returns.

It has been shown in hemp (*Cannabis sativa*), which is a dioecious plant, that by controlling the number of light hours to which the plants are exposed, it is possible to call forth stamens on pistillate plants, and pistils on staminate plants. In the common species of hemp it has not been shown that there is an XY pair of chromosomes in the male, but in another species an XY pair is said to be present.

If then the female plant is XX and if such a plant should produce pollen grains each one would carry one X. McPhee, who tested the pollen on a female plant, found evidence from the sex ratios that all the pollen grains are alike, since only female offspring were produced when this pollen was used to fertilize normal eggs.

Conversely, if the male hemp plant develops ovules there should be two kinds of ovules, one with the X-chromosome, the other with the Y-chromosome. McPhee obtained some evidence that the reversed male does produce two kinds of eggs.

Somewhat similar evidence has been found in frogs by Witschi and by Crew; and in toads by Harms and by Miss Ponce. Exceptionally, hermaphrodite frogs are found. From one such individual Witschi obtained ripe eggs and sperm, and showed by suitable tests that each egg carries an X and each sperm also carries an X. In other words, the frog was a female with two X-chromosomes, and accordingly each egg and each sperm carried one X-chromosome. Crew obtained similar results with another hermaphrodite frog.

In the male toad there is an organ at the anterior end of each testis, called Bidder's organ. Harms and Miss Ponce have removed the testis, leaving the Bidder's organ. After two years this organ developed into an ovary with normal eggs.

One of the most extraordinary cases of sex reversal is shown by the flies belonging to the genera *Miastor* and *Oligarces*. The adults consist of male and female flies which appear once in the course of a year. The fertilized eggs of these flies develop only as far as the larval stage, and then each larva produces new larvae from its eggs that develop by parthenogenesis. A succession of these paedogenetic larvae follows throughout the rest of the year.

Now Dr. R. G. Harris has isolated single, individual larvae, and repeated the process through later generations. In this way a number of pure lines were obtained.

When the paedogenetic cycle ended and adult male and female flies again appeared, all the offspring of any given line became either males or else females. This must mean that half of the lines that had been reproducing as parthenogenetic females were potentially male in adult stages. Furthermore, Harris has shown that external environmental factors determine whether an egg is arrested in development and goes no further than the larval stage (in which case the larva produces eggs) or whether it develops into a fly, which may be either male or female.

So far we have gone over familiar ground. My only excuse for doing so is that experience has shown that these fundamental conceptions of genetics are not widely understood by zoologists and botanists who are working in other fields. It seemed, then, necessary to clear the ground of possible misconceptions before passing on to the more direct attempts that have been made to connect genetics and physiology. The most familiar of these is concerned with the rôle that enzymes play in the development of the characters of the individual.

ENZYMES AND GENES

On the genetic side the suggestion that the development of certain characters is due to the action of enzymes is to be found in some of the earliest contributions after 1900—the date of the discovery of Mendel's paper.

On the physiological side the work with melanin pigments in animals and with anthocyanin in plants goes back at least as far as the last decade of the last century.

On the embryological side the work parallels, in point of time, that of modern genetics. I should like now to discuss this genetic and embryological work in some detail, because it brings out some of the intimate relations of genetics to developmental physiology.

The earliest reference in the genetic literature to enzymes is found in Cuénot's "2nd Note" in 1903 in which he speaks of a chromogen basis ("mnemons") as the substance necessary for the production of all color, and of

specific diastases that determine the particular color that develops.²

In Bateson's second report to the Evolution Committee of the Royal Society, the subtitle reads: "Experimental Studies in the Physiology of Heredity" (1904). He meant no more, I think, than that the characters of the varieties of stocks and peas are physiologically distinct. At least there is no further reference to any physiological process involved in heredity either in this or in the three following reports. But in the fifth report to the Evolution Committee (1909), Miss Wheldale, one of the contributors, has a "Note on the Physiological Interpretation of the Mendelian Factors for Colors in Plants." Following up her previous papers (1909), in which it had been suggested that various red and blue plant-pigments (anthocyanins) are oxidation products of substances of the nature of flavones (the agents of oxidation being oxydases), she reported that white and cream varieties of stocks (and of sweet peas) contain a colorless flavone (chromogen). She suggests that the colored varieties of these plants contain this chromogen in certain stages of oxidation (page 27). These views were put to chemical tests and certain conclusions arrived at concerning the nature of the chemical agents determining the colors and the absence of color.

It is not necessary to go into the many difficult chemical problems that arise in connection with work of this kind. For present purposes it is only necessary to point out that the enzyme nature of the problem was fully realized. From this earlier work onwards there are occasional references in genetic papers, both on plants and animals, to the chemical processes involved in the production of character differences, more particularly color; because color lends itself more readily to studies of this kind. Zoologists have been about as active as botanists, more

²In this connection it is important to note that even at this early date Cuénot suggested that the distinctive feature of albinos is that they do not develop (or inherit) the chromogen but may contain one or more of the diastase-producing factors.

especially as to the development of melanins. The discussion about melanins turns on the oxidation of tyrosin by tyrosinase, and similar problems.³

In more recent times Goldschmidt's important work on sex intergrades in the gypsy moth calls for particular scrutiny. Goldschmidt has made use of an enzyme hypothesis to explain sex-intergrades and has proposed a theory of sex based on the assumption of two enzymes—a postulated male enzyme, or andrase; and a postulated female enzyme, or gynase. The presence of these enzymes is not derived from chemical studies—andrase is little more than a symbol of maleness and gynase of femaleness, but if this is kept in mind the hypothesis may be found useful in describing the kind of results he has observed.

Following an earlier scheme, in which certain arbitrary values are ascribed to "high" and "low" females and males, he assigns certain numerical values to the potency of the enzymes—values which are the initial values, I presume, since they are supposed to change their assigned numbers as development proceeds, as when andrase overtakes and suppresses the effects of gynase or vice versa.

This theory Goldschmidt calls a quantitative theory of sex, but as there are no measured quantities in the amounts of enzymes postulated and only arbitrary values assigned to them, and no measurements from which the quantities can be deduced, the results are as little quantitative, in fact, less so, than the statement that in ordinary cases two X's make a female and one X a male.

As I have said, embryology has run a course parallel to that of genetics in the attempt to apply an enzyme theory to developmental phenomena. The chemical

³ Riddle's rather extensive criticism in 1908 of Cuénot's earlier attempt to utilize enzyme action in the physiological development of color characters, while rather wide of the mark in most respects, had one merit at least in that he emphasized the fact that students of the physiology of melanin pigment had shown that a great variety of colors may result from one and the same reaction according to the point to which the oxidation is carried.

study of the melanin pigments during the last decade of the last century had shown that tyrosin is the principal chromogen involved in the process and that an oxidizing enzyme, tyrosinase, can change tyrosin into melanin. Dewitz's results (1902) on development of dark pigment in the larva of a fly (*Lucilia Caesar*) marked a step in advance. He demonstrated the presence of chromogen in the larvae, which in the presence of an enzyme is oxidized to form the black pigment of the adult.

But a more direct application of chemical theories to development has come from another side, and the question from the start became entangled with a related one, namely, the autocatalytic theory of development.

Van't Hoff in the "Lectures on Theoretical and Practical Chemistry," after pointing out that most chemical reactions are increased in rate three or four fold by a rise of ten degrees Centigrade in temperature, asked whether similar relations may hold in the development of living things, more especially in growth.⁴ Karl Peter attempted to answer this question in 1905 by a study on rate of development of the eggs of the sea urchin at different temperatures. He found a rather close agreement between theory and fact, not only for the cleavage stages, but for later stages as well. He said, "Chemical work during the development of an animal shows the same acceleration at a higher temperature as does a chemical reaction."

Two years later (1907) Loeb suggested that each nucleus is a center of autocatalytic changes, and Wolfgang Oswald independently made the same suggestion. In 1908 Robertson made a careful study of growth, as an autocatalytic change; and in the same year Oswald made comparisons between the two.

A more direct attempt to obtain critical measurements for a study of autocatalytic processes in embryological development was made by Loeb and Chamberlain in 1915. They carried out an experiment on the tempera-

⁴ Quoted from Karl Peter.

ture coefficient of development of the eggs of *Arbacia*. It was generally known that the time elapsing from the moment of insemination to the moment of the first cleavage is constant for a given temperature. But all the eggs of a given female do not begin to segment at the same moment—there is an interval between the first egg that segments and the last. Assuming that the time of division is determined by the “mass” of enzymes in different eggs, it follows that the difference in time is an expression of a corresponding difference in the mass of enzymes in different eggs, those dividing in 100 minutes having more enzymes than those that take 102 or 103 minutes to divide. This means that the mass of enzymes varies in inverse proportion to the time required for cell-division at a given temperature.

The authors stated that “this would mean that the hereditary factor determining the rate of cell-division consists of determiners for definite quantities of ferments.”

We are not here concerned with the validity of the reasoning on which the experiment was based. The question for us is, whether the observations prove that the difference between the cleavage of the first egg and the last egg depends on hereditary factors or determiners. As far as I can see, the eggs might have slightly different amounts of enzymes (or of other kinds of substances in fact) when they are ripe, without these differences having any immediate connection with differences in hereditary factors.⁵ Another kind of analysis, genetic in short, would be necessary to prove this point; the differences in question might perfectly well be due to slight differences in time of ripening of the eggs or to their previous location in the ovary, etc. If so, the differences are not hereditary in the usual sense of the word.

I mention this paper by Loeb and Chamberlain, particularly, because it has been referred to later as having

⁵ While the postulated enzymes may have come originally from genes it does not follow that the amount of the enzymes present in different eggs is a measure of the genes themselves that have produced the enzymes.

shown that the hereditary factors vary quantitatively, but in fact it proves no such thing. Granting all the authors claim as experimental results, the differences appealed to are differences in the eggs at the time—perhaps in the cytoplasm. But this tells us nothing as to whether the genes in the nucleus were at the time (or previously) quantitatively different or not. The reaction may be in fact many stages removed from the gene.

It is in the study of growth that the enzyme theory has received most attention.

Now, as I have pointed out, the growth of animals and plants has been found to depend on genetic differences. In the most striking cases, a single genetic factor-difference may determine whether a given plant will be tall or dwarf. This does not mean that even when a single factor for growth distinguishes one type from another, there are not also many other factors for growth present. It means only that a tall and a short plant differ in one important genetic factor for growth, and that the two have all the other growth factors in common.

Robertson and others have discussed very fully the rate of growth from the chemical standpoint of autocatalytic reactions. Emphasis has been laid on the sigmoid curve of growth (Fig. 3) that bears a striking resemblance to the curve of a uni-molecular, autocatalytic reaction (Fig. 2). Since growth must involve many different processes, and complex chemical reactions that take place now in one region of the body and then in another, it would be more than hazardous to assume that the growth process represents a single unimolecular, autocatalytic reaction. The difficulty has been realized by Robertson, and he has tried to meet it by his second hypothesis of a master-reaction that controls or limits the time rate of all other reactions. The symmetry of the upper and lower halves of the curve of growth shown in Fig. 2 and that of the autocatalytic curve shown in Fig. 3, can not be used as direct evidence of the relationship of the two curves, for this would hold only under

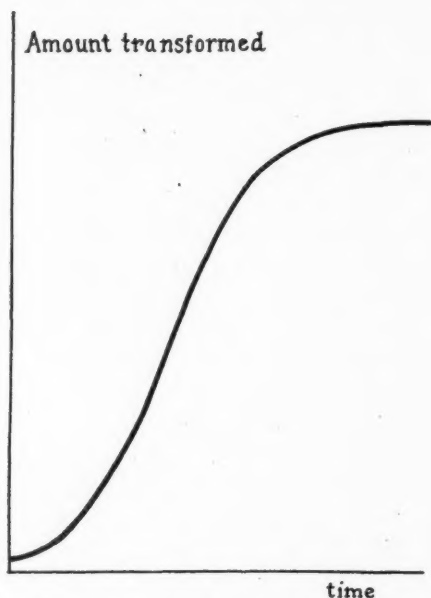


FIG. 2. Curve of an autocatalytic, mono-molecular reaction.
(After Robertson.)

special conditions, *i.e.*, in a closed system. In an organism that is growing and receiving food from outside there is no reason for supposing that the upper half of the curve should be the reverse of the lower half; or even that there should be an inflexion in the curve. Only on the assumption that the reaction is reversible and unimolecular in both directions can symmetry be expected in this case. Robertson has discussed this question for other growth curves that are not symmetrical. He accounts for these cases by assuming that the whole curve is a composite of a few symmetrical curves representing successive and independent cycles of growth. As Plunkett points out, any such sigmoid curve may actually be a composite of a great many independent autocatalytic reactions, consequently the whole concept of a master reaction is unnecessary to account for the observed facts.

Granting that Robertson's interpretation is one of the most suggestive working hypotheses as yet proposed, it does not follow that the autocatalysts of growth need be genes, even if in the final analysis the differences in the rate of growth are traceable to differences in the genes.

The problem is exactly the same as when color differences, that are known to be genetic, are shown to be connected with enzyme action; for the enzymes might, for all we know to the contrary, be many stages removed, in a chemical sense, from the genes that initiate the chain of reactions that come to an end in the final reaction.

From this point on we shall have to be more careful of our terminology. The word autocatalytic, as applied to growth, may mean no more than that a process begins slowly, then proceeds faster and faster and in a closed system finally slows down. Unless some further mean-

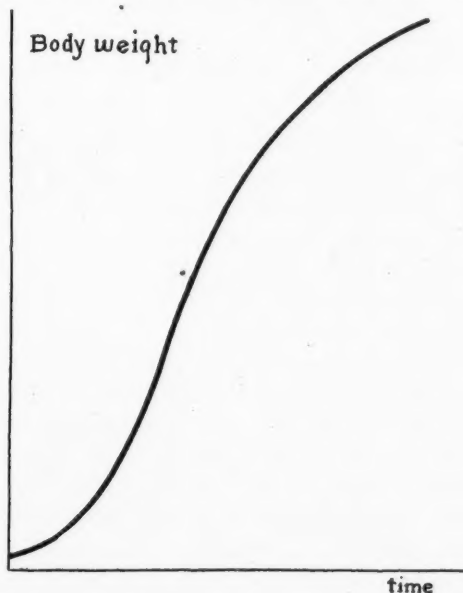


FIG. 3. Curve of the relationship of body weight to age of the white rat, constructed from the measurements of Donaldson. (After Robertson.)

ing can be read into it, the word means only that a plant or animal grows at a rate that at first increases and then decreases. To call this familiar event, autocatalytic, is, in one sense, only to give it a Greek name; but in another sense it is an expression of faith that such phenomena in the organism may be capable of a chemical interpretation.

I am in complete sympathy with this point of view, or, if you like, with these articles of faith; but I can not avoid pointing out that one runs a certain risk in over-emphasizing these resemblances. For even should a process give indications that it is autocatalytic in so far as its data follow a sigmoid curve, the particular factors that enter into the process may be only a matter of conjecture; and, after all, it is the specific character of developmental processes that we now most urgently need to discover.

THE EXPONENTIAL CURVE AND THE GROWTH OF CHROMOSOMES AND GENES

There remains still to be considered the extremely interesting and important theoretical question whether the growth of the chromosomes themselves (and by implication the genes that are their most important constituents)—whether their growth is or is not an autocatalytic phenomenon. This view has been discussed by Troland ('14, '17) for the Weismannian determinants, and by Bridges ('22, '23) and Muller ('22) for the genes.

At the first division of the egg each chromosome divides. Each then grows approximately to its former size.⁶ The amount of chromatin has nearly doubled. At the next division the same process repeats itself. There is four times as much chromatin as at first. The increase

⁶ While the number of the chromosomes is doubled after each division the daughter chromosomes may not grow to the size of the original ones. This again may depend on the size of the cells into which the chromosomes pass. The text refers rather to the geometric increase in number. To what extent the volume of the chromosome is a measure of the size of the genes contained within them is at present unknown.

goes on in a *geometrical series*—and gives an exponential curve, like the first part of the typical, sigmoid curve.

This may be expressed in another way by saying that the process is of such a kind that it becomes more and more accelerated, because more and more chromatin is present as cell-division proceeds.

This does not mean that each chromosome grows faster, but only that there is an ever-increasing number of chromosomes to grow. Taken as a whole, the system is of such a sort that, at an ever-accelerated speed, it reproduces its material. The process resembles at least the first part of an autocatalytic curve.

When the cleavage has divided the material of the egg to a certain point, let us say until one thousand cells are present, the division rate slows down. In this respect the cleavage of the egg may seem to offer an analogy with the second part of the autocatalytic curve.

Let us suppose now—for the sake of the argument—that the genes are enzymes. What would this mean if the process by which chromatin increases is an autocatalytic one? Now our knowledge of enzymes is based mostly on extra-cellular enzymes. In cases of extra-cellular, autocatalytic reactions, in which enzymes are involved, the enzyme itself does not increase in amount. The reaction is said to be autocatalytic, but one of the products of the reaction (which may be an acid and not the enzyme) is the autocatalyst. It is due to confusion, or to forgetfulness of this fact, that zoologists have been led to postulate that the genes are enzymes. In their laudable desire to get to the bottom of their results they have sometimes overlooked the way in which enzymes are supposed to work, and have ascribed to them imaginary properties that are chimerical rather than chemical.

We know, however, that enzymes *are* made by some living cells in unlimited quantities. If there is no proof that they are made as the result of the presence of an initial enzyme of the same kind (for enzymes are not

known to act as autocatalysts of themselves), it would seem plausible to assume that they must be made from some protein or other constituent of the cell—possibly by an action of the genes.

While, then, we may not be warranted in speaking of the genes as enzymes, the genes may be protein bodies, one of whose activities is to produce enzymes which, being set free, act in each cell, and take part in catalytic reaction in the cytoplasm.

A provisional conclusion of this sort would raise another problem of some theoretical interest. The process by which the genes themselves increase after each division to the original size might be regarded as the same process as that by which they affect development. This might mean that the substances of the genes themselves are the same substances that they set free. On the other hand, we might suppose, equally well, that in the resting stages of the cell the genes carry out a process different in kind from that by which they themselves grow, and it is during the resting stage that enzymes (or other substances) may be produced that are set free in the cell. It remains for the future to decide whether these purely speculative ideas have any value as working hypotheses in the analysis of developmental phenomena.

I am afraid that I have spent too much of my hour in criticism of the attempts that have been made to identify the genes with the catalysts of development. I may even seem to have taken an unsympathetic attitude toward the enzyme theory in general, and to the autocatalytic theory in particular. I am sorry if this is so, because I should have wished to produce exactly the contrary effect. If I have seemed critical it is because the questions involved are of the first importance, both for genetics and for development.

The study of the fundamental problems of embryology by experimental methods had almost come to a standstill until two new methods of procedure appeared above the horizon—one the direct application of physico-chemical

methods to the developing organism; the other, the application of genetics to problems of development. The combination of these two methods holds for us, at present, I believe, the most promising mode of attack on the problems of developmental physiology.

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HOMOLOGIES AND ANALOGIES BETWEEN FREE-LIVING AND PARASITIC PROTOZOA

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AMONG the methods of classifying animals is that of dividing them into groups according to their mode of existence. It is thus customary to recognize (1) marine animals that live in the salt waters of the sea, (2) fresh-water animals that live in streams, ponds and lakes, (3) terrestrial animals that live on land, and (4) parasitic animals that live upon or within the bodies of other animals. The major habitats may be subdivided almost indefinitely.

Parasitic animals are often considered apart from free-living species as though there existed some more fundamental difference than that of habitat. It is the object of this paper to compare the structure, life cycles, habitats and activities of the free-living and parasitic Protozoa and to point out that the same principles govern both types of organisms.

The activities of all animals may be separated into (1) those necessary for the maintenance of the individual, and (2) those necessary for the maintenance of the race. The individual must be able to protect itself in its environment, to escape enemies, to reach a favorable situation in which to live, to find, capture, ingest, digest and assimilate food, to egest undigested material, to secrete protective substances, digestive juices, etc., to carry on respiration and to excrete waste products. Races are maintained by the asexual reproduction of the individuals of which they are composed or by sexual reproduction or by both of these processes.

The phylum Protozoa is usually divided into four classes, Sarcodina, Mastigophora, Sporozoa and Infu-

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soria. The Sporozoa are all parasitic; the other three classes include both free-living and parasitic species. It seems probable that the parasitic habit has evolved from the free-living habit independently in each of these three classes and this type of evolution has no doubt taken place many times within each class. Changes from a marine to a fresh-water habitat and *vice versa*, involving the formation of new species, have doubtless similarly occurred among free-living species.

AMÆBA PROTEUS VS. ENDAMÆBA COLI

Let us select a parasitic Protozoon living in man to compare with a typical free-living species. The most common amœba of man is *Endamœba coli*, which lives in the lumen of the large intestine and occurs in about 50 per cent. of the general population. The best known free-living amœba is *Amœba proteus*. Morphologically these two species resemble each other very closely. Both consist of cytoplasm, which is differentiated into an external layer of clear ectoplasm and an internal mass of granular entoplasm. Both possess a single nucleus; the nuclei of the two species differ from each other in shape, size and the distribution of the chromatin, but the differences are no greater than those between nuclei of species belonging to different genera of free-living amœbæ. Both carry on locomotion and capture food by means of pseudopodia; and there is no reason to believe that the fundamental process of amoeboid movement differs in the two species.

The food of both species consists, so far as we know, of solid particles in the medium in which they live, and these food substances appear to be selected in both species; *Amœba proteus* feeds on minute aquatic plants, other Protozoa, bacteria and other animal and vegetable matter that it encounters in fresh water, whereas *Endamœba coli* feeds on bacteria and animal and vegetable matter that occur in the contents of the intestine. Food vacuoles are formed in both species into which digestive juices are secreted from the surrounding cytoplasm and

in which digestion takes place, the digested material being assimilated and the undigested material extruded through the surface of the body. Respiration takes place through the general body surface. The waste products of metabolism are excreted through the ectoplasm. The only striking difference between the two species morphologically and physiologically is the presence of a contractile vacuole in *Amæba proteus* and its absence in *Endamæba coli*. The functions of the contractile vacuole are supposed to be principally respiratory and excretory, functions that in parasitic species are satisfactorily performed through the surface of the body.

The habitats in which *Amæba proteus* and *Endamæba coli* live differ in many respects. The factors of the environment of the former are well known to every student of biology but not so those of *Endamæba coli*. This parasitic species has for its habitat the lumen of the large intestine. Here it lives in total darkness, in the liquid contents, which consist of digested food substances, bacteria of various sorts, the products of bacterial decomposition and more or less changed secretions from the intestinal wall and digestive glands. This medium is more viscid than water and chemically much more complex. The temperature is relatively high and constant (98.6). Peristalsis, which transports the contents towards the rectum, tends to carry the amœbæ out of the body, just as currents of water may transport *Amæba proteus* from place to place. On the whole the environment of *Endamæba coli* is much more constant than that of *Amæba proteus*, but the important points are that each species maintains itself successfully in its own particular environment and that there are no fundamental differences between these environments. If either species is transferred to the environment of the other it is very quickly killed, but both species may be grown in artificial cultures. *Amæba proteus* may be grown in the laboratory in a flat dish containing pond weed immersed in water. The cultivation of *Endamæba coli* requires more care, but has recently been accomplished by several in-

vestigators. The culture medium consists of hens' eggs and Ringer's solution and is very easily prepared. Specimens of *Endamæba coli* are placed in the culture fluid and incubated at 37° C. Because of the rapid growth of bacteria new cultures must be made and inoculated at frequent intervals (approximately twenty-four to forty-eight hours).

The processes of reproduction are not fully known in either *Amæba proteus* or *Endamæba coli*. We know that both of them multiply asexually by binary division and that this division is by a sort of mitosis, but without the dissolution of the nuclear membrane. Sexual phenomena may be exhibited, but none has yet been established with certainty. Cysts have been described in the life cycle of *Amæba proteus*, but appear to be of uncommon occurrence. The animal is reported to become spherical and then to secrete a resistant wall about itself. Within this cyst a large number (500 to 600) nuclei are formed by repeated division of the original nucleus, and each of these nuclei becomes the center of a minute cell or amœbula. These amœbulæ break out of the cyst and develop into recognizable *Amæba proteus* in about three weeks. The cysts of *E. coli* are similarly formed. All food material is first extruded; then a cyst wall is secreted; and finally the nucleus undergoes three successive divisions resulting in eight daughter nuclei. At this point in the life cycle the cysts are carried out of the body in the feces of the host and no further development occurs unless they are ingested by a proper host and are in this way again brought into a favorable environment. The cysts of *Amæba proteus* must likewise encounter a favorable environment before they will develop normally. The process of excystation has not been worked out in *E. coli*, but presumably each cyst gives rise to eight small amœbæ which, as in the case of the amœbulæ of *A. proteus*, grow into adult amœbæ in their natural habitat—the contents of the large intestine. In *E. coli* the cyst wall undoubtedly protects the organisms from injury during their life outside of the body; the cyst wall

of *A. proteus* probably also serves to carry this species unharmed through periods of adverse circumstances.

Endamæba coli is known as a commensal, that is, a species that "eats at the same table" with another species. Man is the other species in this association and *E. coli* is sometimes spoken of as a "food robber" because it ingests food particles that might otherwise be utilized by the human body. The environment within the intestine changes from time to time according to the nature of the food taken in; for example, the intestinal flora may be changed from one consisting almost entirely of acidophilous bacteria to one made up of almost 100 per cent. of putrefactive bacteria by changing from a vegetarian diet to a meat diet for a few days. The intestinal environment may also be modified by the infection of the host with other parasitic organisms such as other species of amebæ, intestinal flagellates, intestinal worms or vegetable organisms such as yeast and *Blastocystis hominis*. Drugs of various sorts and other agents may likewise change the medium in which *E. coli* lives, for better or for worse. How similar are the conditions that exist in the free-living environment of *A. proteus*! The medium in which it lives may be diluted by rain or concentrated by drought. The nature and numbers of other organisms with which it must share its habitat differ from time to time; and pollution of the water may alter unfavorably its surroundings, just as the administration of drugs may modify the intestinal contents of man to the detriment of *E. coli*.

We know nothing about the behavior of *E. coli* within its habitat, but it is safe to assume that this species reacts to stimuli in its environment and that these reactions are such as to insure its continued existence, otherwise the race would cease to exist. These reactions are no doubt different from those of *A. proteus*, but they lead to the same result. The conclusion is inevitable that in morphology and in every process and activity that occurs during their life cycles no essential differences are evi-

dent between the free-living *Amæba proteus* and the parasitic *Endamæba coli*.

A consideration of the geographical distribution and methods of dissemination of the free-living and parasitic amœbæ is also of interest. *Amæba proteus* seems to be very wide-spread, having been found in bodies of fresh water in many countries. *Endamæba coli* is likewise cosmopolitan in its distribution, occurring in man wherever it has been looked for. The factors that control the distribution of the two species are different in certain respects, but the end result is the same. Both species are spread by running water, *A. proteus* mostly in the active stage and *E. coli* in the cyst stage whenever water is polluted with cyst-containing feces. There is evidence that *E. coli* is also carried to the food or drink of man by flies and we know it to be transported to all parts of the world by its human host. *A. proteus* is no doubt carried from one pond to another by aquatic birds and by other organisms and may also be transported by man on aquatic animals or plants.

OTHER HUMAN PROTOZOA

Similar comparisons could be made with similar results between other species of free-living amœbæ and the other five species of amœbæ that live in man. The structure, life cycle and activities of the seven species of so-called intestinal flagellates could be compared with free-living flagellates and the same conclusions arrived at. It seems unnecessary, however, to describe in detail the similarities and differences between these types of Protozoa, nor to discuss in like fashion the six species of hemoflagellates (trypanosomes and leishmanias), three species of blood-inhabiting Sporozoa (malarial plasmodia), the intestinal sporozoon (*Isospora hominis*), the intestinal ciliate (*Balantidium coli*) and the muscle sporozoon (*Sarcocystis*), all of which use some part of the human body as a habitat. Certain characteristics in the lives of these organisms may, however, be referred to with profit.

TISSUE INVASION

Balantidium coli is a large ciliate protozoon that occurs in over 60 per cent. of pigs and has been reported from monkeys. It is an occasional inhabitant of the large intestine of man, especially in tropical and subtropical countries. It is very similar to the common free-living protozoon, *Paramæcium caudatum*, and could be compared with this species just as *Endamæba coli* has been compared above with *Amæba proteus*. One very interesting activity in the life cycle of *B. coli* is its invasion of the tissues of the intestinal wall and the production of ulcers and dysenteric symptoms. The evidence available indicates that it actively bores its way into the tissues, which are apparently dissolved by ferments secreted by the ciliate. Other species of human Protozoa invade the tissues of the host and are thus pathogenic; among these are *Endamæba histolytica*, which causes amœbic dysentery, *Trypanosoma cruzi*, the causative agent of Chagas' disease in South America, *Leishmania donovani*, the etiological agent of kala-azar in the Orient, and the malarial organisms which penetrate the red blood corpuscles. There is no activity among free-living Protozoa exactly like this; otherwise they would be classed with the parasitic species. The invasion of tissue is thus a characteristic peculiar to the latter.

SYMPTOMS

The effect of parasitic Protozoa on their environment, the host, is in many cases very striking, since not only are changes which constitute what we call disease produced but often the death of the host results. Symptoms are nothing but the results of the functional modification of the organs of the host. These modifications are frequently due to secretions of the parasite. That free-living Protozoa bring about modifications in the medium in which they live is well known and the changes observed in the medium correspond to the symptoms resulting from parasitic activities. In other words, the host is an environment just as a body of water is an environment.

NATURAL RESISTANCE

Each host offers certain obstacles which must be overcome by the parasite before invasion is accomplished; in many cases, in fact, hosts do not become infected at all, because of the natural resistance of the body, although parasites succeed in gaining entrance to the intestine or blood stream. We may compare the host with a pool of water which contains various substances in solution and also various species of plants and animals. Not all free-living Protozoa succeed in populating such a pool of water due to the natural resistance offered by the composition of the water and the other organisms present—the physical, chemical and biological factors of the environment. Those that are able to live and reproduce may be said to have successfully invaded this particular habitat. Each species of animal has an optimum habitat; this for a parasitic protozoon is a favorable host and for a free-living protozoon a body of water with certain physical, chemical and biological characteristics.

ACQUIRED RESISTANCE

One of the effects of the infection of animals with parasitic organisms is the production by the host of an active (acquired) resistance which may result in the destruction of many and often all of the parasites and the immunity of the host to subsequent infection. This resistance may be a lytic agent that dissolves the invading organism or, as in the case of the rat trypanosome, may take the form of a reaction product that inhibits the reproduction and hence the multiplication of the parasite. I know of no type of resistance similar to this that may be acquired by the environment of free-living Protozoa; only living organisms are capable of this type of reaction. However, both parasitic and free-living Protozoa may “foul their own nests” by their secretions and excretions to such an extent as to make their respective environments unfit for further life activities. In this way cultures of free-living species may die out and infections with parasitic species may come to an end.

LATENCY AND RELAPSE

An interesting phenomenon characteristic of many parasitic infections is the cessation of symptoms for a time, followed by the appearance of symptoms again, that is, a relapse. An excellent example is that of the malarial parasites which bring about "chills and fever"; these symptoms may disappear spontaneously or with the aid of therapeutic agents, but a few parasites still remain in the body and these, when conditions become favorable again, succeed in bringing about the reappearance of "chills and fever." Everyone who has collected Protozoa from any particular pond at various times from year to year knows that a condition resembling relapse exists in such an environment. Sometimes a certain species is very abundant; at other times specimens can be found only by patient search.

HOST-PARASITE SPECIFICITY

This is one of the most characteristic phenomena in animal parasitology. The parasitism of more than one species of host by one species of protozoon is comparatively rare. Among human Protozoa the ciliate *Balantidium coli* apparently can live in the intestine of both man and pig, and the blood-inhabiting species may live in animal reservoirs or pass part of their life cycle in an invertebrate host, but most of the protozoan parasites of man are restricted, at least in some stage of their life cycle, to life in their human host. There is plenty of opportunity for human Protozoa to invade lower animals and for those of lower animals to invade man, and cross invasion no doubt takes place very frequently, but the environment in one species differs sufficiently from that in another species to prevent cross infection. Just what environmental factors are responsible for these differences is little understood.

HABITAT RESTRICTIONS

The situation as regards free-living Protozoa is quite similar. A particular species has its optimum habitat;

it may even exist although the environmental factors depart considerably from the optimum. There is, however, a point beyond which existence is impossible; life in a habitat where this point has been reached for one or more factors therefore ceases and the species concerned can not grow and multiply in such a habitat, no matter how frequently and abundantly specimens may be introduced into it. Many of the terms familiar to parasitologists might with equal force be applied to free-living Protozoa; for example, a tolerant host or habitat is one in which a protozoon can live and multiply successfully, whereas in a refractory host or habitat life and multiplication are difficult; a natural host or habitat is one in which a certain protozoon generally is to be found in nature, whereas a host or habitat in which a species can not live is considered foreign. Conditions are similar as regards accidental or transitory hosts or habitats and facultative or obligatory species of Protozoa.

CONTROL

And finally, if we wish to control the Protozoa either in man or in a free-living habitat, we apply similar methods. For example, when a person has an attack of amœbic dysentery due to the presence in his intestine of large numbers of specimens of *Endamæba histolytica* he is treated with a therapeutic agent, such as emetin or Yatren; and when a reservoir of water becomes overrun with flagellates of the genus *Synura*, thus causing obnoxious odors and tastes, it is treated with a dose of copper sulfate.

Cases could be multiplied almost indefinitely bringing out homologies and analogies between free-living and parasitic Protozoa, but the above discussion is, I believe, sufficient to prove that the same principles govern both these types of organisms as regards morphology, physiological processes, life cycles and their relations to their physical and biological environments.

REMARKABLE ABUNDANCE OF A CISTELID
BEETLE, WITH OBSERVATIONS ON OTHER
AGGREGATIONS OF INSECTS¹

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MOTORING southward along the east coast of Florida during late June some of the most conspicuous plants along the highway are tall Yuccas. There are many large and especially splendid specimens growing in the sand dune region of Anastasia island just south of St. Augustine. On June 27, 1924, the Yucca flowers were much past their prime, although those of a smaller species which we had been seeing for several days in the country to the northward were just coming into bloom and their flowers, which remain well closed during the daytime, were abundantly supplied with Yucca moths. The large Yuccas of the Florida east coast are abundant in places where they form conspicuous groups, but they are much scattered and one may travel for miles without seeing any examples. At St. Augustine there were a few insects visiting the flower panicles and among these considerable numbers of a small Cistelid² beetle.

Just south of Palm Beach numerous Yuccas began to appear in the landscape and a stop was made to examine them. Every panicle on these plants, which we determined as *Yucca aloifolia* L., was simply swarming with the same Cistelid beetle. Removing one stalk with its enormous panicle of drooping flowers and shaking it vigorously in an insect net I was able to dislodge several handfuls of the beetles which were chloroformed and pre-

¹ Contribution from the Entomological Laboratory of the Bussey Institution, Harvard University, No. 254.

² As this is not a taxonomic paper, I have retained the family name Cistelidæ so long in use, instead of Alleculidæ which by nomenclatural rules will probably replace the former.

served for later examination and counting. Never before have I seen such an agglomeration of insects, except perhaps in a tropical termite nest or a bivouacking colony of driver ants.

The beetle proves to be *Hymenorus densus* Lec. as determined by Casey's revision of the Cistelidæ³ and by further comparison with Leconte's type which is in the Museum of Comparative Zoölogy at Cambridge. The species was described from Florida and has since been reported from as far north as southern Indiana and Ohio. I can find only one reference to its habits and its fondness for Yucca flowers which it probably visits to feed upon the pollen or soft tissues. In his paper on the Coleoptera of Florida, Schwarz ('78) lists this species from Cedar Keys and New Smyrna with the note "common on blossoms of Yucca in June." The beetles were too numerous to be actually counted but as 100 weighed 1.156 grams and the whole catch amounted to 114.41 grams, it includes about 9,888 individuals. As a considerable part escaped, a conservative estimate of the beetle population of a single Yucca panicle would be about 15,000. As there were dozens of Yuccas in flower nearby and many more within sight a more enthusiastic collector might easily have secured a million or more beetles within an hour or two.

Another species of *Hymenorus* has recently been reported as gregarious by Watson ('18; '22). His observations which relate to *H. obscurus* Say were also made in Florida where the beetles frequent the trunks of citrus fruit trees. They feed in the early morning and late afternoon upon "lichens and similar growths," resting during the day in a dense mass that blackens the trunk of the tree. Such groups may contain hundreds of beetles. On occasion the beetles may feed also upon the tender green growth of the citrus trees.

The larval habits of *Hymenorus* appear to be very imperfectly known. Those of *H. rufipes* have been found

³ *Ann. New York Acad. Sci.*, Vol. 6, p. 107 (1892).

in the nests of ants (*Formica* and *Aphaenogaster*) by Schwarz ('98), as well as the pupæ of *H. obscurus*. As Schwarz has indicated they are probably not myrmecophilous since the larvæ of *H. rufipes* and of others have been found living beneath bark.

A search of the literature for specific examples of a similar nature relating to immense numbers of adult insects congregated during feeding has not been very fruitful and has impressed upon me the desirability of securing data concerning the actual population of common insects which exist under normal conditions. Entomological literature includes many references to the unusual abundance of certain kinds of insects at specific times and places and of course the concrete basis of nearly every problem of economic entomology depends upon some such occurrence. However actual counts or careful estimates of numbers are strangely lacking as such matters are usually examined in the light of damage done without close attention to the numerical strength of the destructive insects.

As this matter is of considerable interest I have attempted to add as an appendix to the foregoing brief note a very sketchy summary of the conditions associated with unusual abundance and to cite a few striking cases. Some of these are widely known and others have remained unnoticed or excited little comment.

Ordinarily cases of excessive numerical prevalence of insects are periodic in nature as are those of most animals and even of certain diseases whose epidemiology is at present not well understood. Such periodicity among animals is variously laid to the activities of parasites, abundance or scarcity of food, meteorological conditions, etc. Even sun-spots were held responsible in the early eighties of the last century by Swinton ('83) and this hypothesis has recently been revived by Elton ('25) who has adduced further evidence.

However complicated the basic causes of this periodicity may be, such undoubtedly exists and is frequently

very pronounced. Outbreaks of forest insects like the larch saw-fly or the *Dendroctonus* bark-beetles in North America and the gipsy or nun moth in Europe are typically of this type, exhibiting long quiescent periods. The North American tent-caterpillar (*Malacosoma americanum*) and white marked tussock moth *Orgyia leucostigma* are similar but the outbreaks are usually separated by much shorter periods. Among such insects the outbreaks or epidemics occur at more or less widely separated intervals dependent probably to a great extent upon the abundance of parasitic insects and the rapidity of growth and recovery of their host trees. It may be noted also that they often cover large areas or that the successive appearances need not involve the same locality.

Other cases of abundance are primarily associated with migration or dispersion. These have been most commonly observed in Lepidoptera like the monarch butterfly (*Anosia plexippus*) swarms of which have been observed either before, during or after autumnal migration at one time or another by many American entomologists. I well remember one in the fall of 1899 near Austin, Texas, which so completely enveloped a large pecan tree that its branches drooped and the color of its foliage was replaced by the dull tint of the myriad butterflies which rested with wings folded upon its branches and twigs. No attempt was made to estimate the number of butterflies in this case, but it undoubtedly ran well into the thousands. Williams ('23) in several papers has made observations on the migration of other butterflies in the American and African tropics. Among the various types, it appears that the swarms are usually smaller than those of *Anosia*, although sometimes mounting into thousands and possibly into millions. The large size and brilliant colors of butterflies of course render such swarms much more impressive than those of smaller inconspicuous insects, and many earlier observers have dealt with such occurrences. Tothill ('22) believes in the case of the fall webworm *Hyphantria cunea* that some

outbreaks may be initiated by migrations or flights of moths.

Insects which are not readily disseminated by flight or otherwise frequently appear regularly in great abundance within circumscribed areas. One of this sort is the periodical Cicada or 17-year locust which appears in countless numbers, not every year it is true, but when the adults of each generation mature. As is well known, the distribution of each of these broods is very definite and the appearance of each swarm may be very accurately predicted. In the case of the periodical Cicada the distribution does not appear to be dependent upon the type of vegetation or soil although determined by these to some extent. The suddenness of the appearance of the Cicada is naturally greatly heightened by the fact that its immature stages are hypogæic and that the swarms are not of annual occurrence. Nevertheless their actual numbers are very great. Marlatt ('07) who has studied this species intensively states that the ground beneath a fair sized tree (20 x 20 feet) may bring forth from 30,000 to 40,000 insects as he has counted 84 emergence holes on a superficial soil area of one square foot. Considering the very large size of the Cicada this is really a stupendous quantity.

Insects of amphibiotic habits like the stone-flies and may-flies frequently appear in great swarms, transforming simultaneously in large numbers from aquatic nymphs into winged images. The swarming of the winged sexual phases of ants and termites is a similar phenomenon since it involves the simultaneous movement of a large population from a subterranean to an aerial environment.

The congregation of insects in large masses is frequently a feature of hibernation and has been most often noticed in Coccinellid beetles. These Coleoptera overwinter in the imaginal stage and may either congregate near the scene of their summer's activities or they may migrate into adjacent mountainous country. There are

many published notes on the abundance of these beetles on mountains in both Europe and North America and even in parts of the world as remote as New Zealand. The most remarkable account I have seen relates to a common North American species (*Hippodamia convergens*) in California (Carnes, '12). In parts of California melon vines are severely damaged by Aphids which are kept in check by aphidophagous Coccinellids. It has been found by investigation that the mountainous regions of northern California harbor untold millions of *Hippodamia* during the winter. The beetles associate themselves into masses each containing thousands of individuals, hidden in the soil under the shelter of accumulated pine needles. According to Carnes ('12) two men working together may collect from 50 to 100 pounds of beetles in a single day. As each beetle weighs on an average 20 milligrams, such a catch includes from 1,200,000 to 2,400,000 beetles! As the hibernating colonies always select certain situations on sunny well-drained slopes near running water, long experience enables the collectors to locate the "lodes" of beetles with considerable ease.

Vallot ('12) records a still more remarkable case of another coccinellid, *Desoria glacialis*, which he found present in incredible numbers on the surface of a glacier at Chamonix in the Alps. The beetles were distributed over an area of 20 by 200 meters at the rate of 40,000,000 per 4,000 square meters or 10,000 per square meter.

Werner ('13) also has reported Coccinellids congregated on mountains in Europe, Hudson ('05) in New Zealand and many others have incidentally published similar observations. With the members of this family the aggregations are always associated with hibernation and with a desire to seek out an elevated spot. This is evinced even in the smaller overwintering colonies of *Adalia bipunctata* which I have recently observed beneath shutters and windows of my own house near Boston. Here they seem to prefer places of concealment on the upper floors,

although they are not entirely absent on the lower floor. This might of course be interpreted as a purely tropic reaction (negative geotropism) but may be conditioned by moisture, satiety of appetite, lack of food, temperature or more probably by a combination of all these and no real explanation of the autumnal change in behavior can be reached by the simple postulation of an inhibited, intensified or reversed tropism.

Many other beetles that hibernate as adults congregate in masses but seem not to exhibit the tendency to select elevated places. The European Chrysomelid beetle, *Galerucella luteola*, now very widely naturalized and abundant in North America; regularly congregates in masses for hibernation in protected places. According to Marlatt ('08) this species often assembles in such numbers that it is possible to collect them by the quart.

Neither this beetle, nor the coccinellids just referred to, appear to form swarms in order to reach the places chosen for hibernation, but move independently and gradually accumulate. Another Chrysomelid beetle has been seen migrating in swarms in the autumn, I think most likely as a preparation to entering hibernation. This species, *Disonycha quinquevittata*, has twice been observed in immense swarms (Howard, '98; '01) flying along river courses in southern Arizona. No estimate of the number of beetles involved was made by the observer, Mr. Herbert Brown, but it must have been enormous as in one case the insects formed a belt 20-25 feet in thickness and as wide as the Colorado River at this point (doubtless several hundred feet at this season of the year). The second flight observed the following year was descending the course of the Gila River in a belt about fifteen feet thick and 100 yards wide. This swarm continued during the course of two days early in November while the previous flight took place during October.

Among Hemiptera, many of which hibernate in the adult condition, the chinch bug, *Blissus leucopterus*, is a notable example of gregarious habits. These bugs live

upon various Gramineæ and are very destructive to wheat. In the more arid sections of the middle western states they overwinter in colonies concealed in tufts of the common bunch-grass, *Andropogon scoparius*, commonly as many as 1,000 individuals huddled in the shelter of a tuft only three inches in diameter (Headlee, '10).

Similar associations although usually less marked are so common among insects of all sorts that a gregarious tendency at the time of hibernation may be regarded as a very prevalent phenomenon. It is typical, for example, of many Diptera, *e.g.*, *Pollenia rudis*, *Muscina pascuorum*; Hymenoptera, *e.g.*, *Polistes*; other Coleoptera besides those mentioned, *e.g.*, the Carabid, *Brachinus*; Hemiptera, *e.g.*, *Zelus socius*.

In one of the cases cited, *Polistes*, there is no change at hibernation as these wasps are social during the warm season before the colony disintegrates in autumn, so winter association means only a delay of the instinct to separate and undertake the independent founding of new colonies. In social bees like *Bombus*, however, autumn brings about a break in the social régime as the female bumblebee tends to become solitary at this time, in anticipation of her impending return to solitary life during the coming spring when she will rear her first offspring.

The most notable cases of unusual abundance among insects occur in species which live at the expense of agricultural crops. As has frequently been pointed out these outbreaks are due to changes in environment whereby a great abundance of food is supplied through the extensive growing of plants which serve as specific food for certain insects. When repeated from season to season the opportunities for these insects to multiply increase until the situation becomes economically intolerable. Such cases of excessive abundance do not represent natural biological phenomena although they serve as huge experiments that elucidate the factors which regulate the normal balance of nature among animals. Observations have frequently been recorded which show what the

actual insect population may reach under such conditions of almost unlimited opportunity, but a very few will suffice to illustrate the point. The vast, uniform areas where sugar cane is cultivated in the tropics offer ideal opportunities for the multiplication of cane pests. A cane-boring Scarabaeid beetle, *Dyscinetus bidentatus*, has been described as so abundant in British Guiana by Hutson ('17) that over 4,000,000 were captured with nets in a single season on one estate. In Java, Bernard ('20) has described the great abundance of a slug-caterpillar, *Thosea cervina*, in tea plantations. Over an area of 120 acres as many as 7,500,000 larvæ and pupæ were destroyed and 200,000 individuals were collected in a single day.

Mr. G. W. Barber has kindly allowed me to quote some figures from a manuscript which he has now in press relating to the number of larvæ of the European corn-borer (*Pyrausta nubilalis*) present in corn-fields in Massachusetts. During the year of its greatest abundance in 1922 counts made by Mr. Barber indicate that the population of larvæ per acre may reach as high as 1,100,000 in sweet corn and 1,174,000 in field corn. When present in weeds of various kinds, including barnyard grass, on very fertile soil their numbers may reach 400,000 per acre.

Throughout the great corn-belt of the United States there is a common caterpillar, the corn ear-worm (*Heliothis obsoleta*), which is almost everywhere so uniformly present that practically every ear in the field is infested, almost always by a single caterpillar or at most by two (Quaintance and Brues, '04). It is thus easy to calculate that the population per acre of this insect commonly rises to about 35,000 individuals.

Among insects affecting the cotton plant similar conditions prevail. A very abundant moth, *Alabama argilacea*, known as the cotton leaf-worm, feeds in the larval stages upon the foliage of cotton. This species is widespread in the cotton growing districts of the United

States, but appears never or at least very rarely to overwinter there. It is abundant in the West Indies and each season's crop is thought to result from an early migration of the moths which undergo several generations each summer. In the autumn a northward migration of the last brood of moths continues beyond the cotton belt and often as far as New England and eastern Canada (Gerould, '15). Such flights are very extensive and lead to no advantage as they remove the moths completely from their normal habitat. This is a very patent case of an instinct manifested in an utterly purposeless way at one season while its adaptive nature in the spring might seem equally evident. So far as unusual opportunities for securing food are concerned, there is another insect which has become abundant much as have agricultural pests. This is the housefly.

In his compendium on this species Howard ('11) indicates the numbers of housefly larvae that may develop in specific quantities of food. Thus over 10,000 were counted in fifteen pounds of stable manure in California by Herms who estimated that the population of the manure pile was about 455,000. Many years ago, I secured in a trap almost 100,000 adult flies which emerged from the basement of a fire-engine house where manure was stored, despite the fact that the place had been cleaned as thoroughly as possible by men with shovels previous to the installation of the trap. The housefly is of course one of the most abundant insects in the vicinity of human communities but appears to be more numerous than it really is on account of its fondness for human society. And it still holds its own although hard pressed by the automobile and farm tractor.

The immense swarms of migratory locusts which appear regularly in certain parts of the world have from time immemorial been the most spectacular examples of insect abundance and population counts or estimates have been frequently made.

In Anatolia, Syria and Palestine there was a great invasion of migratory locusts in 1915, due to several spe-

cies. In western Anatolia, according to Bücher ('17), some 6,000 tons of eggs and 11,000 tons of locusts were collected during three months. From the known weights of other species, these amounts would represent about 18,000 billion eggs and 88,000 million grasshoppers, numbers so vast that it is utterly hopeless to grasp their significance.

Workers in the Federated Malay States in their campaign against destructive locusts have recorded (South, '14) the amounts of insects collected which, calculated in actual numbers, show that one day's catch included something over 100 million specimens. In another instance a nearly equal amount was obtained from 65 swarms, indicating well over one million individuals in a swarm. As about 10,000 swarms were destroyed in these Malay States during a single year soon afterwards, it is evident that even such wholesale destruction does not permanently reduce the locust population. Similar occurrences in North Africa (Mancheron, '14) and other parts of the world subject to locust invasions are comparable to those just cited. The actual numbers of a grasshopper, *Camnula pellucida*, present in a locality in one of our western states has been estimated by Ball ('15). He found in one heavily infested part of a breeding ground of this species that there were about one billion eggs per acre, or in more readily comprehensible terms, 25,000 to each square foot of soil surface. As these insects hatch they form slowly migrating swarms and one swarm was found to include some three or four billion young grasshoppers distributed over an area of four square miles with fully half of them concentrated over an area of half a square mile. It is further stated that this swarm was insignificant in extent to one previously observed at the same place.

Among other insects which are general feeders like the locusts may be mentioned the large common "June beetles" of the genus *Phyllophaga* so widely distributed in eastern North America. The adult beetles feed mainly

upon the foliage of various deciduous trees which they assail just at dusk on the warm evenings of early summer. As many as 400,000 beetles were collected during one summer in a small town in Wisconsin (Sanders and Fracker, '16) and similar numbers might easily be obtained generally in many localities in the middle western states.

Excessive numbers of very small insects may readily be present without attracting attention, particularly if they live in concealed situations. Thus the minute gall midge known as the Hessian fly, *Phytophaga destructor*, is widely distributed over the wheat belt of the United States. Its abundance varies greatly, but accurate counts made by McConnell ('21) show that a very moderately infested field harbored over 200,000 larvæ per acre, despite the fact that this number represents less than 5 per cent. of an original population of nearly 5,000,000 per acre which was present previous to decimation by parasites.

The occurrence of insect drift along the beach line of large bodies of water serves to illustrate the abundance of many insects whose numbers are otherwise not noticed. This drift has been commented upon by Needham ('00; '04) and later by several others (Snow, '02; Bueno, '15, and Parshley, '17) and years ago I had opportunity to examine it a number of times in company with Professor A. L. Melander on the western shore of Lake Michigan, where Needham's observations were made. Usually a great variety of insects are present and when conditions are favorable they form windrows on the beach mingled with débris of various kinds. Sometimes one species greatly predominates and in a sample minutely examined by Needham there were over 2,500 crickets (*Nemobius*), 680 grasshoppers (*Melanoplus*) and less than 900 other insects of the most diverse kinds. As such accumulations must be derived from very extensive areas they do not necessarily indicate an originally dense population of insects.

As insects of various kinds are commonly encountered over bodies of water at considerable distances from land, these accumulations result from the drifting shoreward of the bodies of those that fall into the water. A description of several swarms of a large ground-beetle (*Harpalus calceatus*) in the Black Sea by Adams ('08) illustrates the origin of such drift. Swarms of this beetle were met with near the western shore of the Sea of Azof just north of the Black Sea, hundreds were swept from the decks of the steamer and for several days immense numbers were seen floating on the surface of the water. Two weeks later another swarm was in progress.

Accumulations of insect drift are conspicuous in mid-summer along the shore of Great Salt Lake in Utah, but these have a very different origin from those just referred to. They consist almost entirely of the puparia of a small fly, *Ephydra gracilis*. The larvae of this species develop in the highly saline water of the lake and the puparia collect at the surface whence they drift on shore to form a strip often a foot or more in thickness. Aldrich ('12) has described their abundance and estimated the numbers of adult flies that emerged from the puparia and settled upon the beach and surface of the water near the shore line. On the basis of at least 25 flies to the square inch covering a strip 20 feet in width the fly population for every mile of beach would amount to 370 million. Fortunately the flies do not bite. Many of the smaller saline and alkaline lakes of this region and Mexico support large numbers of other forms of *Ephydra*, the preparatory stages of which form an article of diet for the aborigines.

Other small Diptera with aquatic larvæ are sometimes extremely abundant. Certain Chironomid midges commonly become associated in swarms containing hundreds of individuals and these may assume gigantic proportions. The well-known dipterist, Williston ('08) observed them in meadows in the Rocky Mountains "rise at night-fall in the most incredible numbers, producing a noise

like that of a distant waterfall, and audible for a considerable distance."

Very clear-cut cases of migration among the larvæ of small fungus gnats of the allied family Mycetophilidæ have frequently been observed both in Europe and America (Lintner '96). The swarming takes place among the full-grown larvæ which form long snake-like masses composed of thousands of grubs which crawl one over another at a slow rate. The term "Snakeworm" and "Heerwurm" has been applied to these insects which seem always to be species of *Sciara*. The crawling columns may be as long as 10-15 feet or rarely even 30 yards, several inches wide and half an inch in thickness. As the larvæ are about 6 mm. long and 0.7 mm. thick one of these larger swarms about 10 feet in length would include over half a million larvæ.

The attraction of insects to brilliant lights at night is particularly well suited to furnish data concerning numbers normally present over the areas included in the sphere of influence of the lights. As every entomological collector knows, particularly those whose experience dates back to the first general use of electric arc lamps for community lighting, the numbers of insects which appear as if by magic are almost unbelievable. They include a great variety of types, among them very noticeable predominance of certain beetles, aquatic Hemiptera, may-flies, midgets, neuropteroids and to a lesser extent of moths. Twenty-five years ago it was possible to pick up under the street lights of Chicago such beetles as *Calosoma*, *Hydrophilus*, *Cybister* and *Phyllophaga* by the quart and the same was true of the large Hemiptera of the genera *Lethocerus* and *Benacus*. These latter are aquatic forms which are ordinarily rarely taken with the water net although over practically their entire range they are so universally abundant at street lights that they are widely known as "electric-light bugs." Such attraction do brilliant lights offer to many of these insects that after a few years their numbers diminish enormously due

to the vast concourse thus drawn from their natural environment never to return.

With injurious insects that are readily attracted to lights it is a common practice to construct various types of traps fitted with lamps for the collection and destruction of such species. In Europe there are several species of moths which feed as caterpillars on the foliage of grapes and these may be so abundantly attracted to lights that their economic control by this method is possible although expensive. In one vineyard on the Moselle over 18,000 moths were trapped on five nights, and again in another locality nearly 275,000 moths were thus collected from a vineyard of 13.5 acres during a period of a month (Dewitz '12), indicating a population of about 20,000 moths per acre.

Ants and termites are among the most abundant insects and the association of large numbers of individuals in discrete colonies makes it possible to determine actual numbers with considerable accuracy. Yung ('99; '00) has estimated the populations of a number of nests of the European *Formica rufa* and finds that average nests contain from about 30,000 to over 100,000 individuals. The population of the nests of many other species is undoubtedly quite similar, but among forms like the leaf-cutter ants of the genus *Atta* and the carnivorous driver ants (*Eciton*) in the American tropics the colonies are without question many times larger, especially those of *Atta*.

Among termites there are many species that build enormous nests in the tropics of both hemispheres and these form the most populous houses in the world. Andrews ('11; Andrews and Middleton, '11) estimates that the average nest of the common *Nasutitermes* (*Eutermes*) *morio* Latr.¹ of Jamaica, which constructs large arboreal termitaria, houses about half a million inhabitants. With such a nest the "traffic" in and out amounts to

¹ This is referred to by Andrews as *Enterme rippertii*, but the correct name for this form is probably *N. costalis* Holmgren although commonly referred to as *N. morio* Latr. (nec Fabr.)

about 8,000 termites per hour at the time of greatest activity which is shortly after midnight. It may be centuries before an American apartment house can boast of so extensive a human population with such highly coordinated nocturnal activities.

The populations of colonies of the honey-bee is well known and amounts in the ordinary hive to about 30,000 or 40,000 at the beginning of the season. The capabilities of the queen bee for egg-laying are stupendous and observations by Nolan ('25) indicate that she may deposit 1,000 or more eggs each day during her more active period. In addition to the adult bees a colony may contain another 30,000 or 40,000 bees in earlier stages of development (eggs, larvæ and pupæ) bringing the total population to some 75,000 individuals. As the life of the worker bee is at most only a few weeks and that of the male far shorter, rapid multiplication is necessary to keep up the size of the colony. It may be noted that the population of a bee hive is approximately the same as that of the nests of temperate region ants referred to in a previous paragraph although it appears very probable that the life of the individual ant workers is longer than that of the honeybee.

It is seen from the foregoing that conspicuous swarms or aggregations of insects may be due to one of several quite distinct causes.

The populous colonies of social insects are an attribute of social life and their size appears to be limited mainly by the food supply, for the reproductive capacity of such colonies to produce eggs is enormous.

A very considerable proportion among the observed cases bear a more or less direct relation to migration or dispersion and this is true even of the marriage flight of the sexual phases of ants and termites. Among insects preparing for or undergoing hibernation they are a clearly marked expression of the tendency for many non-social forms to become intensely gregarious at that time. Migration may commonly be induced by, or at least co-

incident with the necessity for a larger food supply than is available without migration. This is true of the migratory locusts. Migration to a new and more extensive food supply is evidenced by the spring movements of the cotton moth, but as this species resumes its migrations in the autumn and travels far beyond any food supply, the causal relation is very doubtful and undoubtedly only a coincidence, particularly since this species can have found food in the southern United States during only very recent times since cotton was planted there. Movements toward artificial lights if they may be called migrations are not natural phenomena. The presence of insect drift indicates widespread dispersal or migration which bears at least some relation to air currents. Great abundance correlated with an abundant food supply is most clearly indicated by the insect pests of various cultivated plants, but is nevertheless essentially a natural phenomenon, manifested occasionally under feral conditions like the case of the *Hymenorus* described in the opening paragraphs of the present note.

Very frequently the simultaneous emergence of the aerial forms of insects which have developed in the water (may-flies) or in the soil (periodical Cicada) produce swarms which may later become dissipated through dispersal or remain during the brief remainder of their lives at practically the same spot.

The number of individual insects that become associated in these ways is often very large and sometimes assumes stupendous proportions. We know, however, really very little concerning the actual populations of insects as they exist about us, even those whose activities in destroying useful plants have been quite thoroughly investigated. It is principally through great aggregations of one species or another that estimates of actual insect populations have been based.

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THE BREEDING HABITS OF THE TEXAS HORNED TOAD, PHRYNOSOMA CORNUTUM¹

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WHEN one refers to the literature which deals with the reptilian genus *Phrynosoma* in search of information regarding the breeding habits of its component species, one is very likely to come away with the definite idea that the "horned toads" are viviparous. Thus, if you consult Gadow (4) you will learn that they are viviparous; so, also, if you consult Bumpers (1), Hegner (5), Pratt (8) and others. Our knowledge at the present time concerning the breeding habits of the twenty species of *Phrynosoma* is still very incomplete, but at least two are quite definitely known to be oviparous. These are *Phrynosoma blainvillii blainvillii* and *P. cornutum*. Further, it may be stated that those which are not oviparous are ovoviviparous, as the young develop within an egg membrane from which they hatch just prior to birth. This paper deals with the breeding habits of the Texas horned lizard, *P. cornutum*, in an effort to call to the attention of zoologists in general the fact that *P. cornutum* has been known to be oviparous since 1896, and to try once again to kill the tradition of viviparity which seems to haunt the genus.

The first account I find of the true facts concerning the nesting habits of this lizard is given by Edwards (2) (3). In these papers he gives an accurate description of the nest-digging habits. This work was evidently unknown to Strecker (11) (12), for here he gives his excellent account of the nest-digging and egg-laying habits, believing it to be the first account of the performance, fully and quite unconsciously corroborating Edwards. This ac-

¹ Contributions from the Zoological Laboratory of the University of Illinois No. 284.

count is quoted at length by Van Denburgh (13), wherein one will find excellent bibliographies of fourteen species of *Phrynosoma*. The earlier account of Lockwood (6), in which he quotes a friend's description of how a horned toad, "supposedly *P. cornutum*," defended its young, must be discounted, because some other, ovoviviparous, species must have been concerned. So, too, must we discount all books, making the statement that the members of the genus are viviparous. So, too, finally, must we discount the more recent article by Morris (7) wherein he figures what certainly *looks* like *P. cornutum* (though he never names the form he is discussing) and describes how the living young are born.

On the afternoon of May 30, 1921, I was walking in a field not far from the agricultural college at College Station, Texas. Here I chanced upon a female *P. cornutum* standing motionless and on her toes in the center of a grassless, sunbaked area. The rigidity of her posture struck me and I sat down and waited to see what she was up to. The time was about 6:15 P. M. For perhaps five minutes she stood thus, then settled to her normal flat posture, took two steps forward and began very solemnly to dig. The work was leisurely done, but progressed steadily. When the hole was first started, only the front legs were used in digging, the hind legs being spread rather widely, acting as a brace. The scratching was done mostly with the feet operating alternately, but there was little regularity in this: sometimes one foot would make four or five scratches in succession. The rate of scratching, timing by means of a stop watch ten periods of ten seconds each, averaged fourteen scratches in ten seconds. The dirt loosened by the forelegs was thrown both under and to the sides of the belly during the initial stages of the excavation, but as the cavity began to descend, the dirt was further removed by the activity of the hind legs, which ejected it from the mouth of the hole. The ground in which the nest was dug was very hard, and at the end of two hours a tunnel two and a



FIG. 1. Nest and egg complement of *Phrynosoma cornutum*, after the nest had been dug open.

half inches long, extending downward at an angle of about 60° , had been excavated. The lizard paid not the slightest attention to me, so early in the game I moved over and sat with her between my legs the better to watch her operations. She permitted me to measure the hole, submitting to handling without objection, and resumed her digging operations immediately upon being released. By eight thirty it was too dark to see anything clearly; as a matter of fact all there was to see was the slowly disappearing posterior half of a horned toad, with little clouds of sand flying out from under her body. The opening to the hole measured two and five eighths by one and three quarters inches. I carefully marked the location and left her till morning.

When I returned at eight the next morning prepared to dig out the nest, the lizard, of course, was gone, and there was only the slightest trace to mark the spot where I had watched the performance the previous evening. The

hole, too, was gone. A heavy dew had wetted down what little sand remained scattered about after she had filled up the hole. I began feeling with my fingers where I knew the nest must be, and finally detected a slightly less solid resistance where the hole had been. I was much surprised to note how firmly the dirt was repacked into the burrow. Digging revealed the fact that the tunnel descended without turns to a depth of five and a half inches. This terminated in a circular chamber three and one eighth inches in diameter and two and a quarter inches high. In this were laid twenty-seven eggs, arranged in three layers of eleven, nine and seven eggs each. Between each tier was a layer of sand sufficiently thick to keep the eggs from touching, firmly packed in. There was no order or arrangement in the position of the eggs in a tier, save only that all lay horizontally. The eggs were removed, examined and measured. The average size of this set was 16.7 by 10.9 mm; the average of 117 eggs measured by me is 16.9 by 10.8 mm. The eggs

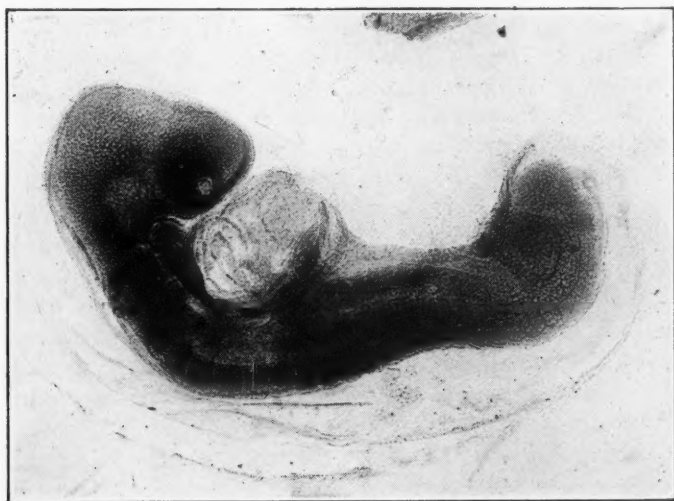


FIG. 2. Embryo of *Phrynosoma cornutum*, showing state of development about eight hours after the egg was laid. Actual size of embryo 1.77 mm.

were creamy white in color, covered with a flexible leathery membrane. Ten of these eggs I preserved in formalin; eight I left with a friend to hatch; the remaining nine I took with me to southern Wisconsin, where they hatched. Those left in Texas hatched on the thirty-ninth day; those I had in Wisconsin hatched on the forty-sixth and forty-seventh day. As both were kept in the original sand, the difference must be due to a variation in the summation of temperature. After nearly five years in formalin, I have removed the embryos from the preserved eggs, and present herewith, as Fig. 2, the state of the embryo found in the egg not more than eight hours after the egg had been deposited in the underground cavern. The actual length of the embryo is 1.77 mm.

The foregoing description is typical of six nests which I have seen in various stages of their construction. There is little variation in the diameters of the tunnels, though there is considerable variation in the depth at which the egg chamber occurs, due partially to the angle of incidence of the tunnel, and partially to the varying conditions of the soil into which the nests are dug. Those dug in relatively soft ground are relatively longer, though the egg chamber is not necessarily farther, vertically, from the surface of the ground. The number of eggs in six sets that I have dug out has been as follows: 27, 24, 25, 24, 23, 25. One further fact is of interest and will bear additional observation: Edwards (3) found his female digging her nest at 6 P. M.; I have observed five females at work, and 5:10 P. M. is the earliest I have found them digging. Data would seem to indicate, therefore, that nest digging is a crepuscular activity, and the egg laying a nocturnal one. This is rather peculiar, as the Texas horned toad is not normally particularly active in the cooler temperatures of the evening.

During the actual mating, the male assumes a dorsal position above the female, much as in the anura, but the amplexus is not nearly as violent, nor does the reflex persist. I once carried a mating pair in my hand for two hours before they separated; on being released, the male refused any further consideration of the female.

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EFFECTS OF AGE OF PARENTS ON CHARACTERISTICS OF THE GUINEA PIG¹

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It is a common belief among livestock breeders that the age of the parents has important effects on the characteristics of the progeny, especially that immature parents produce offspring that are inferior in size and constitution.² As yet, however, there seems to be no clear evidence from experimental data. Supposed effects have also frequently been suggested in man. There is considerable evidence that first babies average lighter in weight and shorter in height at birth than their brothers and sisters, and that the proportion of still-births and of deaths in the first year among them is considerably above the average. The proportion of males also seems to be exceptionally high. The evidence for other characteristics which have been assigned to the first born, such as greater susceptibility to tuberculosis and to the attractions of a criminal career, and greater prevalence of albinism, insanity and genius are based on statistics which seem to fall short of proving any biological difference between members of the same family. An excellent review of the literature is given by Holmes in a chapter in the "Trend of the Race," which he significantly calls "The alleged Influence of Order of Birth and Age of Parents upon Offspring."

In view of the prevailingly negative evidence, the writer has been surprised to find that age of parents (probably of dam rather than sire) is an important factor in such cases as the occurrence of polydactyly and

¹ From the Department of Zoology, University of Chicago, and the Bureau of Animal Industry, United States Department of Agriculture.

² Compare Mumford, 1917, "The Breeding of Animals"

amount of white spotting in guinea pigs. Slight effects on the mortality rates and probably on early weights of the young are less surprising.

The piebald pattern of colored spots on a white ground depends primarily on an incompletely recessive Mendelian factor. There is, however, much variation among strains which possess this factor. The present data were collected from a strain (Family 35 of previous publications³) the recent representatives of which are descended from a single mating in the twelfth generation of brother and sister mating. As might be expected, there is very little genetic variation left within this strain. The correlation between parent and offspring averages only $+ .024 \pm .013$ in comparison with $+ .191 \pm .018$ within a random-bred stock. In spite of this absence of hereditary variation there is still variation from self-white nearly to self-colored, the standard deviation being 19 per cent. of the total area of the coat.

One of the factors determining amount of white is sex. Males averaged 6.7 per cent. more color than females in this family, a result which is close to the average sex difference found in other stocks. Most of the variation is due to non-genetic factors which are different even in litter mates and are thus of a rather intangible sort. There is some correlation between litter mates, however ($+ .103 \pm .018$ in place of $+ .282 \pm .018$ in the random-bred stock). There is no appreciable relation between amount of white and season of birth, size of litter, birth weight or mortality rate. The only tangible factor aside from sex which has so far been found is, in fact, age of dam. The following table shows the percentage of white in young born at different ages of the dam. The age of the sire is the same as that of the dam in the great majority of cases, since nearly all matings were between litter mates.

The probable errors for the age classes are all close to 1.0. The average difference between the young of very

³Wright, 1920, *Proc. Nat. Acad. Sci.* 6: 320-332; 1922. *Bull. No. 1090*, 1121. U. S. Dept. of Agriculture; 1926. *Jour. Am. Stat. Ass.* 21: 162-178.

Age of Dam Months	Males		Females	
	No.	Per cent. white	No.	Per cent. white
3.0-	182	56.3	153	60.5
6.0-	195	59.5	187	67.6
9.0-	152	60.6	160	66.5
12.0-	150	61.3	124	70.6
15.0-	174	63.2	149	69.6
21.0-46.0	138	66.9	144	73.3
Total	991	61.1	917	67.8

immature females (less than six months of age) and those of the oldest group of females (more than twenty-one months of age) is 10.6 ± 1.4 for males and 12.8 ± 1.4 for females. The correlation ratio between age of dam and percentage of white in the sons and daughters averages $.190 \pm .015$. From the square of this figure it is apparent that age of dam determines about 3.6 per cent. of the variation in the piebald pattern within family 35 and is a factor which should raise the correlation between litter mates by .036 above the correlation between parent and offspring. While not very important in determining total variation it is a major factor in the group of non-genetic factors *common* to litter mates.

Guinea pigs reach about half their mature weight at three months of age but continue to grow rapidly to the sixth month, at which time their growth is about three fourths completed. Growth is practically complete at fifteen months. The gestation period averages about sixty-eight days. The present data include records of litters produced by females up to the forty-fifth month of age. In other stocks records as late as the sixty-first month have been obtained. The effect of age of dam on the piebald pattern as far as dealt with here must thus be considered an immaturity rather than a senescence effect.

Guinea pigs in common with the wild species of genus *Cavia* and the closely related genus *Kerodon* have only three toes on the hind feet. An extra toe occurs in occasional individuals. This toe is not a reduplication of one of the other toes, such as is found in the common polydactyly of cats and the occasional polydactyly of man,

but seems to be a real reinstatement of the lost digit V. Castle⁴ was able to produce by selection a race which bred true to a perfect four-toed condition. Crosses between this race, kindly furnished by Professor Castle, and various inbred races in which polydactyly has never occurred gave results which indicate segregation of two or three major genetic factors, the results being clearly different in crosses with different three-toed stocks. One inbred stock, the same Family 35 used in the study of piebald pattern, has produced a considerable proportion of polydactyly from the beginning, although unrelated as far as known to Professor Castle's stock. Considerable differentiation has arisen among the branches of this family with respect to polydactyly even since the twelfth generation of brother-sister mating, the portion of the family considered here. One branch has produced as much as 69 per cent. polydactyls and several about 10 per cent., with the others distributed between. There is in consequence some correlation between parent and offspring ($+ .183 \pm .018$) in contrast with the absence of correlation with respect to piebald in the same family. Within the branches, however, it turns out that three-toe \times three-toe and four-toe \times four-toe have produced substantially identical results. Within such a branch, the occurrence or non-occurrence of polydactyly must thus be due wholly to non-genetic factors. The high correlation between litter mates, $+ .623 \pm .027$ in the data as a whole, reduced to an average of $+ .538$ within branches of the family, indicates that more than half of the non-genetic variation is due to factors common to litter mates in marked contrast with the situation in the case of the piebald pattern. Another contrast is the complete absence of any difference in sex ratio between polydactyls and normals.

In agreement with the piebald case, however, is a marked effect of age of dam. The figures are summarized below.

The significance of the age effect stands out after making all due allowance for the intra-litter and the intra-

⁴ Castle, 1906, *Car. Inst. Wash. Pub.* 49.

Age of Dam Months	Young No.	Per cent. polydaetyl
3.0-	349	52.7 \pm 1.8
6.0-	390	40.0 \pm 1.7
9.0-	319	29.2 \pm 1.7
12.0-	292	26.7 \pm 1.7
15.0-	330	18.5 \pm 1.4
21.0-46.0	296	14.2 \pm 1.4
Total	1,976	31.1

branch correlations in interpreting the probable errors. The decrease in percentage of polydactyly with increasing maturity of the dam is found without exception in each of the twenty-one branches descended from the single foundation mating (twelfth generation of brother-sister mating). The following condensed table shows the results in four groups (A, B, C and D) in which the family branches are combined according to the average proportion of polydaetyls produced by them.

Age of Dam Months	Percentage of polydaetyls			
	A	B	C	D
3.0-	29.3	34.6	68.1	81.0
6.0-	7.4	28.2	54.4	69.5
9.0-	9.6	21.9	28.9	50.0
15.0-	6.1	12.1	22.0	30.2
No.	386	676	498	416
Average	11.9	21.4	38.4	55.8

The correlation between percentage of polydactyly and age of dam (biserial correlation ratio) is $.370 \pm .018$, indicating that 13.7 per cent. of the variation in the family is due to age of dam.

In searching for other factors the most important indication found is a correlation ratio of $.187 \pm .020$ with month of birth. The proportion of polydaetyls produced from November to April (1916 to 1924) was 37.5 per cent. in comparison with 25.5 per cent. in the remaining half of the year, a difference of 12.0 ± 1.4 per cent., which is not appreciably changed on correcting for age of dam and family branch. Apparently polydaetyls are more likely to be produced under unfavorable than favorable conditions. The data indicate a peculiar relation to size of litter, there being a statistically significant excess of

polydactyls in litters of two and three as compared with larger litters and also with litters of one. There are only slight indications of differences between three-toed and four-toed young in mortality percentages and weights.

The question arises whether the apparent effect of age may not be due to birth rank. The data are not well adapted for answering this question since the correlation between age of dam and birth rank (each classified so as to give a linear relation to polydactyly) is very high ($+ .927 \pm .002$). The correlation between birth rank and polydactyly is $-.342 \pm .018$, while as noted above that between age of dam and polydactyly is $-.370 \pm .018$. The partial correlations, $-.427$ between age of dam and polydactyly for constant birth rank but only $-.008$ between birth rank and polydactyly for constant age of dam, indicate as conclusively as is possible from such data that birth rank has no influence except as related to age of dam.

It has been assumed above that age of dam rather than of sire is the significant factor. As already noted the sire and dam were litter mates in the great majority of cases, which thus can give no information on this question. The few cases of marked difference in age all point toward the dam. The most interesting of these is the one case in the data in which a female gave birth to a litter when less than four months of age (one hundred days). This litter was sired by the dam's own sire (seventeen months old at the time), something which occasionally happens when litters are left with the parents to thirty-three days of age as in all of the present data. The three young were all polydactyls. Two of them had perfectly developed fourth toes on both hind feet, the other barely fell short of the grade. Only twenty-nine perfect polydactyls were recorded among the 1,976 animals in the family. Fourteen of these were born before the dam reached her sixth month, twenty-four before she reached her ninth month, and all but one before she reached her fifteenth month. It can hardly be a coincidence that the most perfect poly-

daetylous litter in the entire body of data was produced by the youngest dam.

The excess tendency to develop digit V induced by immaturity of the dam may be looked upon as an "acquired character." The data do not indicate that any hereditary change is induced. Females born from dams less than nine months of age produced 32.3 per cent. polydactyls, while females born from more mature dams produced 30.1 per cent. polydactyls. There were about twice as many polydactyls among the former group of females as in the latter. The small difference between the groups of progeny almost wholly disappears on correcting for the age of the immediate dams and for branch of family.

As might be expected from the common influence of age of dam, three-toed animals have a little more white in their coats (4.4 per cent.) than four-toed. The average difference for a constant age of dam, however, reduces to 0.3 per cent., indicating that there is no other common factor of importance.

In contrast with these marked effects of age of dam on polydactyly and color pattern are the slight effects on a group of characters which *a priori* might have been expected to show greater effects. There is, it is true, a distinct decrease in the mortality rate of the young with advancing maturity of the dam. There are merely indications, however, not conclusive evidence, that birth weight and early gains rise with age of dam. Size of litter and sex ratio show no changes which can be relied upon, although a slight excess of males (above the average ratio) in first litters is in harmony with human statistics as far as it goes.

The nature of the age effects described here is far from clear. Possibly some sort of competition between the growth process of the dam and the early developmental processes of the embryo may be responsible. There seems to be no relation to the very marked effect of pre-natal competition of the young with each other to which a correlation — $.629 \pm .010$ between size of litter and birth

weight (live young) in the present data is largely due. Increased litter size has no effect on the color pattern and appears to have on the whole the opposite effect on occurrence of polydactyly to that of immaturity of the dam. The small effect of age of dam on the birth weight of young further indicates that immaturity of the dam has effects of a wholly different nature from that of prenatal competition between litter mates.

Whatever the nature of these effects, it seems clear that age of parent (probably of dam only) has marked effects on color pattern and occurrence of polydactyly among guinea pigs in which there is a suitable balance of the genetic factors affecting these characters. The results suggest that age of dam may be more important as a factor affecting embryonic development of mammals than indicated by the small amount of previous experimental data brought to bear on this question.

THE FUNCTIONAL SIGNIFICANCE OF THE IN- VERSION OF THE VERTEBRATE RETINA

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ALTHOUGH of all the structures in the animal body the eye presents what is possibly the most impressive example of adaptation it is worthy of note that this organ has been more frequently singled out for criticism than any other on the ground of its alleged structural defects. It was Helmholtz who declared that if the eye had been supplied to him by an optician he would send it back for repairs; and Metchnikoff arrived at the even more unmerciful judgment that "Nature, in fashioning the eye, has blundered at every step."

The inversion of the vertebrate retina presents a problem of no small importance in the philosophy of zoology. It is a matter of common knowledge that the rods and cones of the human eye have their percipient ends directed away from the light and are furthermore situated in the deepest portion of the retina, with the result that the rays of light, before coming to a focus, have to traverse the ganglionic and synaptic layers that constitute the greater portion of the retinal thickness. The collocation of the parts of the retina in this manner has commonly been held forth as an instance of imperfect structural adaptation of the eye towards fulfilling the functions of an optical instrument. It has been pointed out that the percipient elements ought, according to human ideas upon the correct construction of optical instruments, to be turned with their free ends towards the light. It can be urged with reason that the passage of the light-rays through the heterogeneous nervous layers must be attended with some degree of absorption and irregular refraction with consequent detriment to the

sharpness of the image, which would be avoided were the rods and cones to be situated upon the inner surface of the retina.

The inversion, then, of the vertebrate retina has come to be regarded by many as of no functional significance, and so far from being adaptive this feature has been considered the reverse and explicable only with reference to the origin, either phylogenetic or ontogenetic, of the eye.

Not only the mode of development of the retina but also the peculiar origin and relationship of the lens have attracted the attention of biologists in the past. Balfour ('81) and Jelgersma ('06) are to be noted as proponents of the commonly accepted view that the vertebrate retina originated on the outside of the body implanted in that portion of the ectoderm from which the nervous system was destined to develop and was carried in *pari passu* with the sinking of the latter beneath the surface. This view is certainly suggested at once by the ontogeny of the retina; but if ontogeny has recapitulated phylogeny here, the retina, as Parker ('08) points out, must be supposed to be a functional organ during its period of migration from the surface. Parker suggests that in a transparent pelagic ancestor the position of the receptive membrane is immaterial. Balfour offers no suggestion as to any living animal which may represent a stage in the evolution of the eye. Von Kennel ('81) believed that the annelids might throw light on the matter. Jelgersma inclined to Amphioxus.

At all events these investigators agree in believing that the vertebrate retina has arisen from a superficially situated optic organ. Ontogenetically the inversion of the retina arises by the processes of invagination involved, firstly, in the formation of the neural tube from the ectoderm, and, secondly, in the further involution of the optic vesicle from the forebrain. By still further invagination the distal half of the optic vesicle sinks inwards to form the nervous layer of the retina (which includes the pericipient elements), the cavity of the vesicle being ulti-

mately represented by the line of division between the layer of rods and cones and the pigment layer of the adult retina. Thus morphologically the rods and cones have their free ends abutting upon a space which was derived

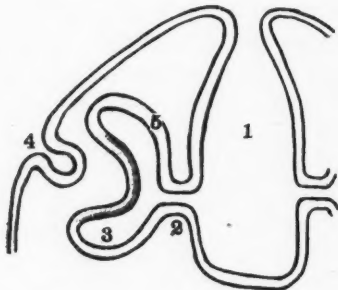


FIGURE 1. Schematic representation of the origin of the vertebrate eye to illustrate the morphological relationships of the percipient elements to the outer ectoderm. The figure represents a transverse section through the head. It will be seen that the rods and cones are situated upon the equivalent of the outer surface of the ectoderm. The ectoderm only and its derivatives are shown. 1, forebrain; 2, optic stalk; 3, optic vesicle; reduced by invagination of the distal half upon the medial surface of which are developed the rods and cones. The latter are indicated by shading (their apices are towards the right). 4, lens vesicle; 5, proximal half of the optic vesicle from which is developed the pigment epithelium of the retina.

by involution of the ectoderm from the outside world (see Fig. 1). Hence, on the recapitulatory theory, the percipient elements are considered to have been situated, at the outset of their evolution, at the extreme surface of the skin, a position in which they would certainly appear to be, of all others, most favorably placed. In certain vertebrates the retinal rudiment becomes apparent during embryonic development at a stage when the neural plate is not yet closed in. But if we assume that the prime tendency of the percipient elements is to turn towards the light it would seem that in the continuity of evolution the retinal rudiment must have migrated away from the central nervous system when the latter sank

below the surface. It would be easy to understand, as Parker suggests, that a very primitive optic organ might accompany the nervous system inwards in a transparent animal; but if the retina is highly differentiated for the perception of form in external objects its position becomes of great importance, since only well-defined dioptric media must intervene between it and the light. It would seem, then, that the eye-rudiment would develop an increasing tendency to remain at the surface.

At all events it is clear that by a very probable and plausible course of evolution (and embryonic development) the eye could be formed with the rods and cones turned towards the light. Supposing that the retinal

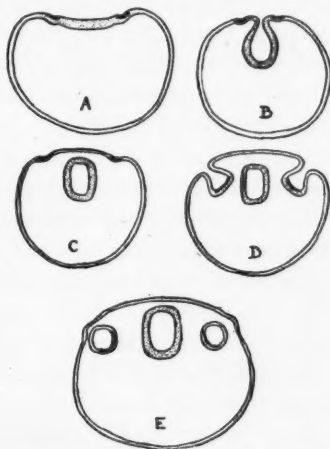


FIGURE 2. Diagrammatic representation of a hypothetical course of evolution in which inversion of the percipient elements would not be involved. The sections are transverse. In *A* the retinal rudiment is included in the primitive nervous plate. The percipient elements, turned towards the light, are shown by short thick lines. In *B* the sinking of the neural plate is inaugurated but the retinal rudiment is left upon the surface. In *C* the closure of the neural tube and detachment of the retinal rudiment are complete. *D* indicates the commencing evolution of the eyeball by invagination, the process not involving inversion. In *E* the optic vesicle is closed and has the rods and cones turned towards the light. It will be noted that it would not be absolutely necessary to postulate initial incorporation of the light-sensory surface into the neural plate; in that case the hypothetical process would be simplified.

rudiment consisted of a portion of the ectoderm some little distance from the neural plate, its subsequent evolution by sinking would be represented in embryonic development by an optic vesicle invaginated directly from the ectoderm in the manner illustrated by the other two principal sense organs, namely, the ear and the nasal organ, which arise as simple pits upon the surface. In other words, if the eye developed in the same way as the other two sense organs the retina would be uninverted (see Fig. 2). And if the inverted retina is a functional anomaly it would seem that had the eye developed by simple invagination from the surface the anomaly would be avoided and that a functionally superior eye would result. Why then has the eye not done so?

It is interesting to note that Sharp ('85), Béraneck ('90), von Kupffer ('94), Burekhardt ('01) supposed that the process we have suggested above did actually occur, but that the primitive retina is now represented by the lens (which, of course, arises as a pit, upon the ectoderm). The lens in its early development resembles the vertebrate olfactory and optic vesicles, and also the rudiments of invertebrate eyes. The primitive retina was supposed to have been modified into a dioptric organ and the deeper nervous layers to have acquired percipient properties and hence a new retina was established from brain tissue. Thus the present retina is secondary.

This theory has few adherents. The difficulties, as Parker points out, of converting a ganglionic mass into a new retina are very great. Moreover, such a view offers no explanation of the inversion.

Lankester ('80), on the other hand, believed that the eye arose in the central nervous system, in a position comparable to the eye of the ascidian larva. Boveri ('04) assigned the origin of the vertebrate retina to the numerous pigment spots of *Amphioxus*. Parker favors Boveri's theory; he points out, however, that, apart from the theories of Balfour and Jelgersma, no attempt has been made to account for the most striking characteristic

of the retina, namely, its inversion. Parker then proceeds to account for the inversion by enlarging upon Boveri's view that the vertebrate eye is homologous with the sense spots of *Amphioxus*. He refers to the work of Hesse ('98) who showed that the pigment spots of *Amphioxus* are in the form of cups in which percipient nerve-endings are found, the percipient nerves entering by the mouth of the cup. The sensory elements of the retina are held to be derived from these pigment cups and the inversion is explained by the fact that the cup must be turned with its mouth towards the light to allow the light to enter. Such an arrangement implies that the percipient nerve-ending must be turned away from the light.

Parker, however, does not refer to the structure of the retina in the pineal eyes of *Lacertilia*, described at length by Spencer ('87). In *Hatteria*, to take the most illustrative example, the pineal eye contains an undoubted retina, with rods, pigment, nuclear and molecular layers and nerve fibers running to the central nervous system. But in the pineal eye the retina is uninverted: the rods are situated upon the internal surface of the retina with their free ends *towards* the light (that is to say, towards whatever light may be considered to enter this rudimentary organ).

In view of the uninverted condition of the pineal retina it would appear that Parker's theory is by no means the last word on the subject of the inversion in the paired eyes of vertebrates.

Now it is clear that if an adaptive significance could be assigned to the inversion the complexion of the problem might be materially changed. It is the object of the present paper not to deny that the inversion is functionally disadvantageous to the eye regarded purely as an optical instrument, but to show that it may have been imposed as a physiological necessity associated with the peculiar circumstance that the eye, though admittedly an optical instrument, is a living organ in addition.

Attention will be drawn in the first instance to the fact generally accepted in all the theories of vision that visual

sensation is the manifestation of photochemical action taking place in the rods and cones. During continuous vision this photochemical metabolism must be very considerable; in other words the rods and cones require a copious blood supply. The blood volume, which is very considerable, of the vascular tunic of the eye furnishes an indication of the high metabolic requirements of the percipient elements, working unremittingly as they do; and the inference I propose to make is that they are situated upon the outer surface of the retina in order to come into close physical relationship with the blood-supply.

It will be noted (see Fig. 3) that the vascularity of the choroid which is well indicated by the numerous plexuses is most marked precisely behind the area covered by the rods and cones. The high degree of vascularity of the choriocapillary membrane extending against the retina from the ora serrata to the edge of the blind spot indicates indubitably that the blood requirements of the photochemical cells are very considerable. Beyond the ora serrata the plexuses disappear, in the absence of the optic portion of the retina, but are developed again distally to supply the ciliary muscles and the iris. The tunica vasculosa, indeed, must exist almost exclusively for the supply of the rods and cones. The blood-requirements of the sclerotic and the permanent pigment of the choroid must be relatively insignificant to judge from what is known of the normal blood supply of such kinds of tissue, and the sclerotic is furthermore taken care of by the episcleral vessels. The fact the choriocapillary membrane is a dense network of fine vessels pressing close against the back of the retina shows even more plainly that the tunica vasculosa owes its voluminous development to the metabolic needs of the rods and cones.

The inner nervous layers of the retina are supplied by the small retinal vessels circulating in front of the retina, but these are of insignificant dimensions compared with the tunica vasculosa. The disparity between the

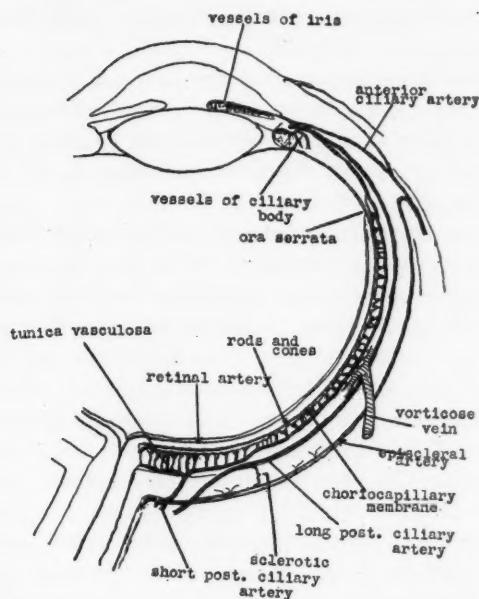


FIGURE 3. The blood vessels of the eyeball, diagrammatically represented. (After Th. Leber.) Only the arteries are shown, in solid black.

two sets of vessels supplying the retina (namely, the retinal vessels in front of the rods and cones, and the tunica vasculosa behind them) is a measure of the concentration of metabolic activity into the rods and cones (and possibly to some extent the pigment layer of the retina). So great indeed is the vascularity of the choroid that under the ophthalmoscope the back of the eye appears of a deep unbroken red.

The conclusion is therefore reached that the blood-requirements of the rods and cones are very high, which is amply borne out by what is known and believed regarding their continuous activity during vision. In further illustration it may be mentioned that behind the fovea centralis, the center of most intense vision, where the percipient elements are presumably most active, the

choroid is thickened by an increase of the choriocapillaris (Piersol).

We have thus seen that the inverted arrangement permits of the retina functioning with a few of its blood vessels against the light, but with the greater part of its blood supply behind the rods and cones *and out of the path of the light-rays*.

In order to illustrate the physiological significance of this arrangement of the parts the argument will be based on the hypothesis of an uninverted retina. Supposing that the rods and cones were turned towards the light in the highly active modern vertebrate eye, so that they abutted upon the hyaloid membrane of the vitreous humor, with the ganglionic and synaptic layers behind them as is found in the obsolete pineal eye of *Lacertilia*: how then is their blood supply to be disposed? That the vascular tunic should be dispersed among the ganglionic and synaptic layers is inconceivable. Even so it would be structurally impossible for the vessels to attain greater propinquity to the light-sensitive ends than the bases of the inner bulged segments of the rods and cones, and the subservience of the metabolic requirements of the apices would be very problematic.

The only answer can be that in an eye of the type which we meet in modern vertebrates, if the retina were uninverted the tunica vasculosa would require to be situated in *front of the* rods and cones, and in the path of the light rays. Only by this arrangement could the blood serve the apices to an adequate degree.

Such a relationship of the parts would however only serve to surpass the departure from optical perfection which may be considered to exist in the inverted retina. In both the matter of actual thickness and of refractive heterogeneity the vascular coat must far exceed the relatively transparent nervous layers in front of the percipient elements in the inverted retina. And this is not to speak of the entoptic effects which would be produced by the hosts of highly refractive red corpuseles in active

circulation between an uninverted retina and the light. Even the delicate retinal vessels, which do circulate against the light, can produce under certain circumstances disagreeable entoptic effects. Apparently, however, the presence of these vessels is necessary for the nutrition of the ganglionic and synaptic layers and the vitreous humor, which are too far away from the choroid; and the retina must tolerate them in front. But if the tunica vasculosa migrated *en masse* to the front to serve a sheet of rods and cones turned towards the light, the result might well be disastrous from the optical point of view.

If the reader will gaze steadily at a blue sky or the empty illuminated field of the microscope he will (after a little patience if not already acquainted with the phenomenon) become aware of numerous bright and dark specks which pursue meandering paths across the field of view. These are distinct from true *muscae volitantes*, having their cause in the refraction of the light by the corpuscles circulating in the retinal arteries. Many people have never noticed this phenomenon because the retinal arteries do not extend in front of the fovea, and most of us have not acquired the habit of assimilating retinal impressions outside the center of distinct vision. If the moving specks are watched closely their pulsations can be detected, so that a practised observer could count his pulse by gazing at the sky. Now it occasionally happens that the retinal arteries can suffer temporary engorgement with blood, as the result of a violent sneeze, for example, the spasmodic compression of the thorax sending a powerful pulse through the anterior arterial trunks. Under these circumstances the retinal arteries are distended for a few moments with large masses of corpuscles whose refractive effect is to give the startling impression of moving sparks around the observer's head. This symptom, also, often heralds an attack of apoplexy where the head vessels are known to be unduly distended.

Now if the extensive tunica vasculosa were in front of the retina instead of behind a permanent and marked

disturbance of vision would be occasioned of the nature just referred to, and on a far greater scale. Furthermore, from the fact that the choriocapillaris is thickest behind the fovea it is clear that a vascular tunic against the light would require to be thickest over the center of distinct vision, since that portion of the retina is the most active. The entoptic disturbance would be most serious at the very place where it would be most unwelcome. The elimination, indeed, of the retinal arteries from the face of the fovea can be regarded as an expression of their unwelcome character in that place, small as they are. Since the retina is very thin at the fovea, owing to the reduction of the nervous layers, the choriocapillaris behind suffices for the nutrition of the whole foveal region.

It would be idle to multiply speculations of this character, but the argument might be summed up by saying that what we might regard as a moral obligation on the part of the rods and cones to turn towards the light has been rendered impossible of fulfilment by the necessity imposed upon them to turn inwards to seek their means of sustenance. No optician would design an eye in which the mass of the nutrient vessels had to be placed against the light. The bird's eye, which is believed to possess the most acute vision of any, has the retinal arteries abolished and replaced by the pecten, which can be moved so that its shadow does not disturb the center of vision. The plate in a camera is placed with its silvered side towards the light (uninverted). Supposing that the chemical processes of photography involved the immersion of the silvered side in some cloudy fluid when the photograph was taken, then the silvered side would have to be turned away from the light with the fluid arranged behind (inverted).

To derive the inverted retina of the vertebrate paired eye from a primitive eye in which the retina is uninverted, such as the pineal eye of *Hatteria*, is not a difficult matter. The pineal eye of *Hatteria* consists of a hollow

sphere on the proximal half of whose inner surface are situated the rods, their apices turned towards the cavity of the sphere, and hence towards the light. The distal half of the sphere bears no rods, but its wall is thickened to form a lens. If now the rods migrate from the proximal half of the sphere round its wall to take up their position upon the distal half, they are still facing the cavity of the sphere but are now turned away from the light. The invagination of the distal half of the vesicle into the proximal half would be precisely what occurs in the development of the paired eye and would result in an inverted retina. But now the outer half of the vesicle wall would not be available for the formation of the lens; therefore the latter must arise afresh, and the most likely place for it to take origin is from the overlying ectoderm.

Returning to the aspects of the adult condition of the vertebrate paired eye it will be realized that two fundamental functional factors were involved in the discussion of the inversion. In the first place, the percipient elements of the retina must be densely crowded together so that no portion of the field is without a percipient unit. Furthermore, the percipient elements must be all placed on the same "focal plane" (which is not necessarily flat but more often curved). Therefore the percipient layer of the retina is equivalent to an unbroken membrane of geometrically even configuration, whose activity presents two aspects. On one side it is in nutritive association with the blood, and from the other side emerge nerve-impulses into the individual nerve tracts of the discrete percipient units. Since on the one hand a voluminous blood supply is involved and on the other the existence of densely crowded nerve tracts, the placing of the percipient layer between is merely an expression of the fact that no other arrangement would be structurally possible. As we have endeavored to show, the placing of the vascular tunic behind, and the nerve tracts in front, leads to the optimum conditions of optical functioning.

Whether the optical advantages of the inverted retina have been sufficiently fundamental to have determined in

evolution the peculiar manner of the development of the eye or whether they have arisen as merely incidental advantages in relation to form of development determined by factors even more fundamental is a problem beyond the scope of this paper to discuss. We may, however, conclude by referring very briefly to the case of the olfactory and auditory organs whose rudiments have not been carried inwards when the nervous system sank below the surface. In neither of these organs, in fact in no other sensory structures, do the same rigid conditions for the architecture of a percipient membrane arise as in the eye. In no other sensory structure is it absolutely necessary for the percipient units to be crowded together so that no portion of a percipient membrane shall be without a unit; in no other organ has a percipient membrane to be formed of geometrically even surface, that is to say one in which no folds, no indentations, no villous projections are to be permitted. Therefore the customary structural devices whereby tissues of different function and kind can be intermingled in a state of subdivision are not applicable to the eye: its involved mode of development may yet be the expression of factors of this nature.

Nor does there seem occasion to treat further here of the ancestral condition of the vertebrate eye, which may have been uninverted as in the pineal eye, or of the eyes of invertebrates in which the percipient units are turned towards the light. Suffice it to say that the inversion of the vertebrate retina would appear to be, in its broadest aspect, the expression of the superior functional activity of the modern vertebrate organ of sight.

SUMMARY

The inversion of the vertebrate retina is functionally adaptive in that the percipient elements, by being placed into close physical association with the vascular coat of the eyeball, which is external to the retina, are situated in that position in which most rapid metabolic exchange

can take place with the blood, in connection with their high photometabolic activity. Arguments based on the hypothesis of an uninverted retina are adduced to show that were the rods and cones turned towards the light the migration of the vascular coat internal to the retina would be necessitated, and that in such a case the presence of a mass of blood vessels between the retina and the light would be detrimental to optical efficiency. The case of the uninverted retina of the pineal eye of *Lacertilia* is discussed. Previous theories relating to the origin of the vertebrate eye and to the inversion of the retina are briefly reviewed; and it is pointed out that no attempt has been made in the past to assign a functional significance to the inversion and that the inversion is very commonly and erroneously regarded as an anomaly.

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SHORTER ARTICLES AND DISCUSSION

THE LETHAL NATURE OF THE "CREEPER" VARIATION IN THE DOMESTIC FOWL

In a paper read at the 1924 meetings of the American Society of Zoologists,¹ Dr. I. E. Cutler called attention to the peculiar variation found in "creeper" fowls, in which the leg and wing bones are shorter and thicker than in normal fowls. In his experience, creepers never bred true, but usually produced some normal chicks, and some chicks with an extreme defect of the legs, in addition to creeper chickens. Matings of creepers by normal fowls usually produced about equal numbers of creepers and normal chickens. Although no detailed data were available, the case appeared analogous to that of the yellow mouse, which always is heterozygous, due to the death of the homozygous yellow embryos early in development.

During the past season we were able to obtain some creeper fowls from Dr. Cutler. Preliminary data from breeding experiments with these fowls indicate that the creeper variation is due to a single dominant gene, which is lethal in the homozygous condition. The evidence is derived from matings between a creeper male and two creeper females, and between the same creeper male and three normal unrelated females. The results are summarized in Table 1. All eggs incubated from these matings were candled at frequent intervals during incubation, and those containing dead embryos were opened and the embryos examined. We were able to classify embryos dying after the fourteenth day as creepers or normals on gross inspection. The distribution of this character as given in Table 1 is derived from descriptions of chicks hatched and reared and of embryos dying after the fourteenth day. The ratios of creepers to normals among the embryos dying late in incubation and among the chicks hatched did not differ significantly.

The proportion of creeper to normal chicks in the offspring of creeper \times creeper matings is about as 3 : 1, although the numbers are too small to be significant, and other considerations indicate that this probably is a departure from a ratio of two creepers :

¹ 1925. *Journal of Heredity*, 16: 352-356.

one normal. From matings of creeper \times normal the ratio probably is 1 creeper : 1 normal. It is certain that all the creepers used were heterozygous, and that the creeper condition is dominant.

TABLE 1

RESULTS OF MATING CREEPER FOWLS *Inter-se* AND WITH NORMAL FOWLS

	Fertile	Dead Embryos			Hatched	Creepers	Normal
	Eggs	1-6	7-13	14-21			
		days	days	days			
Creeper $\delta \times$ Creeper \varnothing	33	15	5	4	9	10	3
Percentage	100	45.5	15.2	12.1	27.3
Creeper $\delta \times$ Normal \varnothing	71	3	12	9	47	30	26
Percentage	100	4.2	16.9	12.7	66.2

Of greater significance, perhaps, is the death-rate of the embryos in the two types of matings. Embryos from creeper \times creeper matings had a very high mortality rate early in incubation (45 per cent. before the seventh day), while embryos from creeper \times normal matings, incubated in the same machine and at the same time, showed a much lower mortality rate (4 per cent.). Mortality at other periods was the same in both types of mating, and the large difference in the percentage of eggs hatched from the two types of mating (27 per cent. for creepers as compared with 66 per cent. for creeper \times normal) is due chiefly to the difference in the early mortality of embryos. We have assumed, therefore, as a working hypothesis, that the high early mortality in the creeper \times creeper matings is due chiefly to the death of homozygous creeper embryos early in development. If this is so, all creeper chickens hatched, including those in which the defect is extreme, should prove to be heterozygous.

Further breeding tests are in progress, as well as a morphological study of the creeper variation, and a comparison of this defect with the chondrodystrophic variation² of chick embryos to which it bears a superficial resemblance.

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² Landauer, W., and Dunn, L. C., 1926, Proc. Soc. Exp. Biol. & Med., Vol. 23: 562-566.

WING PRODUCTION IN PLANT LICE

VARIOUS factors have been considered as affecting the ratio of the winged to the wingless forms in plant lice. Among those most prominently employed in experimental work are: Starvation, temperature, moisture, sunlight, nature of food, parentage and inheritance.

The results obtained by the earlier experimenters in regard to the effect of starvation were confusing; but two recent workers, Wadley (1923) and Ackerman (1926) each, after performing carefully controlled experiments, have come to the same conclusion, *i.e.*, that starvation causes a large increase in the number of winged forms produced, particularly if the starvation period or periods occur early in the development of the individual.

That temperature has a decided effect on the production of winged forms was shown by the writer, Ewing (1916). It was found that in the case of the apple-grain aphid (*Aphis avenae* = *Rhopalosiphum prunifoliae* ?) there was an optimum temperature for the production of the wingless forms and two optima for the production of winged forms—one above and the other below that for the production of wingless forms. These results were confirmed by Wadley (1923), who found, however, that in relation to other factors temperature was of less importance. Now Ackerman (1926) not only finds that temperature is of much importance in affecting the ratio of winged to wingless forms, but that there are two optima for the production of the latter as well as for the former.

Moisture has been but little considered as a factor affecting the dimorphism of asexual aphids except as an element in the food. Probably this is because Headlee (1914) showed that when above 37 per cent. saturation its variation did not affect the rate of metabolism.

Davidson (1924) tested the effect of light, using that from artificial sources, and came to the conclusion that sunlight, temperature and the length of day are probably factors of major importance. His work on the effect of sunlight awaits confirmation, although Ackerman (1926) has tested this factor in relation to its effect on the plants on which the aphids were feeding. He considered that the absence of the normal amount of sunlight might have a starvation effect on the plant louse because of its effect on the nature of the plant juice imbibed. However, aphids born of wingless parents and reared on plants that had been

grown in semi-darkness for a period of four days were all wingless.

Outstanding among the experiments upon the effect of the nature of the food eaten are those that deal with the addition of certain salt solutions to the soil of the growing plant that furnished the food of the aphids. Shinji (1918) has claimed rather remarkable effects for his "wing-developing" salt solutions. Also Clarke (1903) and Neils (1912) claim the effectiveness of certain salts. The more recent results of Ackerman (1926), who used over four thousand reared aphids in his experiments, are entirely negative in regard to the effect of salts. He states: "It was found that when aphids were reared on plants grown in solutions of the 'wing-developing' salts winged forms did not appear in any larger proportions than when they were reared on plants growing in the usual nutrient salt solution."

Shull (1918) noted that parentage had an important effect upon the ratios of the offspring in regard to the presence or absence of wings. He found that the ratio of winged to wingless offspring was liable to be much higher where the parents were wingless than where they were winged. His results have been confirmed by Wadley (1923), Ewing (1925) and Ackerman (1926). It was shown by the writer, Ewing (1925), that this parental effect was cumulative; that a much larger ratio of winged offspring would be expected where there was a long line of wingless ancestors than where there was only a wingless parent or parent and grandparent.

Inheritance in a strict sense, *i.e.*, the transmission of characters through the germ plasm of the parent to offspring, is not known to have any effect on the nature of asexual dimorphs. Not only this, but no effect was found by selection using several variable characters that were independent of dimorphism. This was very evident in the case of a pure line of apple-grain aphid that the writer propagated for eighty-seven generations.

Ackerman (1926) in the development of his theory that "... wing production in the grain aphid is dependent upon changes in the proportion or concentration of certain materials in the haemolymph . . ." showed that: "The fat-globules solidified as the result of exposure to low temperatures (7° to -3°), but the solidified fat-globules of 20° aphids did not melt at a temperature lower than approximately 65° C." Ackerman further holds that this solidification of fat globules at low temperatures is due not directly to the effect of the temperature

change but that the temperature change disrupts certain brown-colored globules, and their discharged material brings about the solidification of the fat. He believes there is a relation to this solidification process and the production of wingless forms. Whether or not this relation is ever proved the discoveries of Ackerman in regard to the effect of low temperatures on causing the solidification of the fat globules in the haemolymph of a plant louse will doubtless be the starting point of much fundamental research into the physiology and nutrition of insects and its possible effects in regard to a number of problems of growth and polymorphism.

In closing it may be well to call attention to the analogy between the production of functional wings in asexual aphids and the abnormal production of wingpads in certain insect larvae, a process termed prothetely. Prothetely occurs more frequently in coleopterous larvae than in those of other orders and has been supposed by some to be induced by sudden or violent changes in environmental factors (Williams, 1914). Sudden temperature changes in particular have been suggested as the chief causes of this phenomenon.

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ON THE TYPE OF GONODACTYLUS SPINOSUS, A STOMATOPOD CRUSTACEAN

In the year 1893 two descriptions were published of stomatopod crustacea that are very much alike. One was by J. R. Henderson, at the time professor of biology in the Madras Christian College, and the specimens were some that he had collected at Rameswaram. This island, famed for its venerable temple, forms the western link in the chain, known as Adam's Bridge, that connects the mainland of India with Ceylon and lies at the northern boundary of the Gulf of Manaar. The other description was by the present writer and was based on two specimens in the U. S. National Museum that had been collected by Colonel N. Pike at Mauritius, an island in the Indian Ocean east of Madagascar.

The specimens from both localities are small, not over twenty-three (23) mm in length and resemble the common *Gonodactylus chiragra* of the Indo-Pacific Region. They differ chiefly in the peculiar sculpturing of the terminal segment of the abdomen, the telson. This bears on its dorsal surface high rounded prominences, separated by narrow grooves, and beset with a variable number of fine spinules.

To his specimens Henderson gave the name *Gonodactylus demanii*, regarding them as specifically identical with a single female that had been collected by Dr. J. Brock at the little island of Edam in the Java Sea near Batavia and that was described and figured without a name by de Man in 1887. The specimens from Mauritius were named *Gonodactylus spinosus*. As pointed

out by Kemp, the first description has priority over the second by one month.

Since 1893 a number of authors have recorded the capture of similar forms at numerous localities along the littoral of the Indian Ocean and its tributaries. So now the distribution of this species may be said to extend from Mauritius on the south to the Gulf of Suez, the Red Sea, and Persian Gulf on the north, and from Zanzibar and the Ibo Archipelago, Portuguese East Africa, in the west to the Sea of Java in the east. Outside of this region Kemp (1915) reports specimens of typical *G. demanii* in the collection of the University of the Philippines from Palawan; and Borradaile has described a form under the name *Gonodactylus spinosus* from Rotuma, an island in the southern Pacific north of Fiji. Kemp regards this as a variety of *G. demanii* because it differs from the typical form only in the entire absence of spinules upon the telson.

All the specimens that have been classed as *G. demanii* or its varieties are small in comparison with other Stomatopoda. The largest, so far as I know, is a specimen 43 mm in length reported by Kemp and Chopra from the Gulf of Suez. Most specimens are under 30 mm, and Henderson mentions a male only 12 mm long that appeared to be mature. They all agree in certain structural characters but show considerable variation in the form and proportions of the telson, and especially in the number, arrangement, and shape of the minute spinules on the dorsal surface.

In his valuable monograph on the Stomatopoda of the Indo-Pacific Region (1913), Kemp recognizes *G. spinosus* as a distinct variety of *G. demanii*, basing the distinction mainly on the differences in the relative breadth of the telson. In the addendum to this paper (p. 198) he describes another feature common to all the specimens that he had collected at several localities at the northern end of the Gulf of Manaar.

This is the entire absence of setae on the inner margin of the inner uropod, and he calls attention to the fact that this feature is clearly shown in Henderson's figure of the type specimen. All other specimens in the Indian Museum, except one from the Persian Gulf, showed the usual complete fringe of setae.

Again in the specimens from the Philippines, Kemp (1915) found the same absence of setae as in those from the northern part of the Gulf of Manaar. Later, in a collection made by Mr. Cyril Crossland in the Red Sea, Tattersall found some specimens with and some without the setae, and regards this as the best distinction between the typical form and variety *spinosus*.

Quite recently I have had occasion to read the discussion of this subject by Kemp and Chopra (1921). These authors are inclined to agree with Tattersall, but find no precise correlation between degree of spinulation of the telson, size of the lateral teeth, and presence or absence of the fringe of setae. On the other hand, the fringe of setae is either present or absent (like Mendelian allelomorphs) on the inner margin of the inner uropod; intermediate forms do not occur. Specimens without the setae can without doubt be referred to the typical form of *G. demanii*, since this feature is shown in Henderson's figure. But it was uncertain whether specimens having the complete fringe can be identified as *G. spinosus* Bigelow, because no mention was made of setae in the descriptions of the type.

Fortunately I am now able to supply this deficiency. For in my possession, through a generous loan from the United States National Museum, is one of the two type specimens of *Gonodactylus spinosus* Bigelow (U. S. N. M. No. 4295). This specimen is a female, 21 mm in length on the median line. The accompanying figure (Fig. 1) of one uropod and part of the telson will answer the question raised by Kemp and Chopra. It will be seen that this specimen presents nothing peculiar in the arrangement of the setae, the fringe being complete on both branches of the

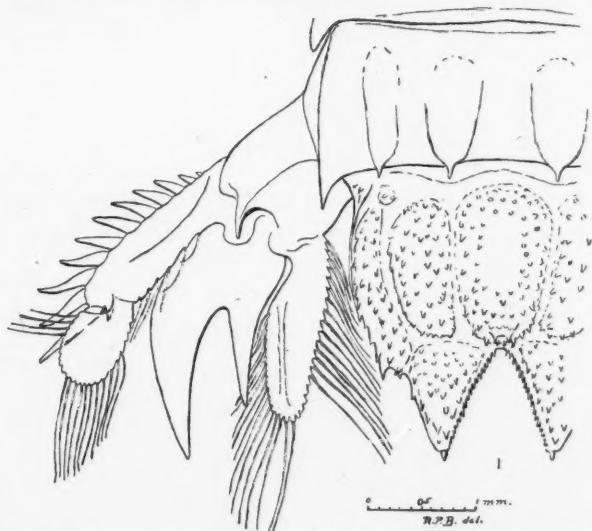


FIG. 1.—Left uropod, with parts of the telson and sixth abdominal somite, of the type specimen of *Gonodactylus spinosus* Bigelow. (U. S. Nat. Mus. No. 4295.) Outlines drawn with camera, details freehand.

uropod. The specimen is slightly damaged; but, where the setae have been rubbed off, the articular indentations are perfectly distinct. The setae are distinctly pinnate, but it was not possible to represent the very fine lateral branches on the scale of the drawing.

Reexamination of the specimen furnishes opportunity to add a few other particulars to the previous description. The articulated spines on the outer margin of the proximal segment of the outer branch of the left uropod are eleven and there are ten on the right limb, not nine, as previously stated. The proximal spine is minute, and binocular dissecting microscopes were not in use in 1893. The terminal fixed spine on this segment is also very small.

The width of the telson is 2.8 mm; its length over all 2.8 mm, and on the median line is 1.7 mm. The outlines are drawn with great care. The surface of the elevations is perhaps somewhat rougher than indicated in the drawing.

The very small, transverse dorsal processes of the ophthalmic somite (Fig. 2) are partly covered by the spine of the rostrum,

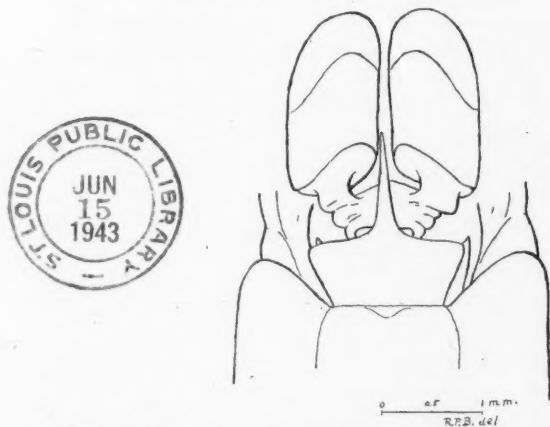


FIG. 2.—Eyes, rostrum and part of carapace of the same. Camera drawing.

their outer angles appearing in dorsal view between the base of the spine and the anterior lateral margin of the rostrum. This margin is slightly in advance of the rounded anterior lateral lobes of the carapace.

ROBERT P. BIGELOW

MARINE BIOLOGICAL LABORATORY,
WOODS HOLE, AUGUST 9, 1926

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